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CONTENTS.

A. Brindle

The Larvae and Pupae of the British Cylindrotominae and Limoniinae (Diptera, Tipulidae)

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Department of Biology, University of Salford.
N. D. RILEY, C.B.E., F.Z.S., F.R.E.S.
7 McKay Road, Wimbledon, London, S.W.20

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J. H. KENNAUGH, M.Sc., Ph.D.
Department of Zoology, The University, Manchester 13

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The Larvae and Pupae of the British Cylindrotominae and Limoniinae (Diptera, Tipulidae)

Brindle, A.

ERRATA

It has been noted that an error occurs on page 156, on the eighth line up from the bottom.

In this line the word NEMATOCERA should be substituted for DIPTERA.

This mistake on the part of the author, is much regretted.

TRANSACTIONS OF THE SOCIETY FOR BRITISH ENTOMOLOGY

VOL. 17 AUGUST 1967 PART VII

The Larvae and Pupae of the British Cylindrotominae and Limoniinae (Diptera, Tipulidae)

By A. Brindle
(Department of Entomology, Manchester Museum)

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1. Introduction

The present paper forms the second part of a survey of the immature stages of the British Tipulidae, the first part of which dealt with the subfamily Tipulinae (Brindle, 1960). The present paper deals with the identification of the larvae and pupae of the other two subfamilies of the Tipulidae, so that the two parts attempt to cover the known immature stages of the family.

In the part dealing with the Tipulinae, the numbers of species included were comparatively small, and since most of the larvae and pupae were known, it was possible to give keys to species. This is also possible with the Cylindrotominae, but in the Limoniinae the numbers included are much greater, and there are still many species unknown in the immature stages, so that in

general the keys to this subfamily are given to genera or to species-groups only. However, since one-fifth of the known genera contain one species only, a key to genera is much more useful than might have been the case, and in certain genera or subgenera, such as *Limnophila* s.s., only one of the species is common and widely distributed, whilst the other species is rare; in these cases, it is the common species which has been included. Keys are also given to the known species in some of the larger genera, so that in practice the keys should serve to identify all the species in the small genera, and the more common species in the larger genera, with the exception of those in the Eriopterini. Although the known genera of this tribe can be separated as larvae or pupae, only a few species of *Ormosia, Erioptera,* and *Molophilus* have been reared.

The characters given in the keys to genera refer to known larvae and pupae, and it has been assumed that these characters will hold for larvae and pupae not yet known. This seems reasonable since the characters cover the larvae and pupae of American species described by Alexander (1920), and the details of the pupae of *Oxydiscus* and *Ormosia* are taken from this source. The larvae and pupae on which the keys are based, however, are clearly mentioned in the text; it can be assumed that any larva or pupa not mentioned is unknown, as far as the author is aware.

In the smaller genera, the larvae and pupae not yet known are listed, but this has not been done for the larger genera, such as *Limonia, Ormosia, Erioptera,* and *Molophilus,* since this would include most of the species on the British List.

Since the object is to enable the non-specialist to identify the immature stages, the keys are designed to make use of external characters, which are quite adequate to separate the genera, and often to separate species. The details given are those considered useful for identification purposes, and comprehensive details are not included. The characters of the mouthparts have not been used, since comparatively few larvae have been adequately studied, and to include available details of the mouthparts of the genera in the present paper would add greatly to its length without contributing to its main purpose. Therefore only a very brief and general account of the mouthparts is included.

Relatively few references are given at the end of the paper, and these are restricted to those having a direct connection with the present study; for further references Alexander (1920), Hennig (1950, 1952), Crisp and Lloyd (1954), and Lindner (1959) should be consulted.

A check list of the 39 genera and species-groups recognised as British is given on pp. 213, and of these 34 are included in the larval and pupal keys. The five genera not included (see check list) are either unknown in the immature stages, or have been inadequately described.

The classification follows that of Coe (1950) in which the Cylindrotominae forms a very distinct, very small subfamily, and

the Limoniinae is divided into four tribes. The genera are taken as in Coe (*l.c.*) but the subgenera are only dealt with separately if the larvae and pupae show distinctive characters, as in *Limnophila*; otherwise the genus is considered as one unit, as in *Limonia*. In one subgenus, *Pilaria,* there are three well defined larval and pupal types, so that each of these is considered separately as a species-group.

The classification of Coe (1950) is followed without any implication that it is correct in a phylogenetic sense, though there seems to be little doubt that it is basically sound. The only difficulty may be in the heterogeneous genus *Limnophila,* which is certainly diverse, but this fact alone does not necessarily indicate that the classification is unsound. The phylogeny of the subfamilies is not considered in the present paper. The genus *Ula* was placed in the Hexatomini by Brindle and Bryce (1960), following Alexander (1920), but the genus is here placed in the Pediciini as in Coe (*l.c.*). The sole difference between the latter publication and the present paper with regard to nomenclature and classification is that the subgenus *Trichyphona* of Coe (*l.c.*) is here raised to generic rank, and certain species included in the subgenus *Trichyphona* in Coe (*l.c.*) are here dealt with under *Dicranota,* following Brindle (1963). This change is made on account of both larval and adult characters.

In order to avoid unnecessary repetition of such phrases as "the larva of" or "the pupa of", the species name alone is often given. A reference to a family, subfamily, tribe, genus or species, refers to the larvae or the pupae according to context. If the adults are meant this is stated.

2. Methods

Collecting

With the exception of those referred to in the text, all the larvae and pupae described in the present paper have been personally collected from various localities in a number of counties of Britain, mainly from the North-Western counties of England.

The standard method of collecting most of the larvae and pupae of the Limoniinae has been by means of a sieve. This is a standard sieve sold by ironmongers for sieving flour; the one used is of 12″ diameter, with 16 meshes to the inch. The soil to be investigated is placed in the sieve, and sieved in any convenient stretch of water, when the soil passes through the sieve and leaves any larvae or pupae behind. The limitation of this method is that the soil should be reasonably near water, but the advantage of the method is that relatively large areas of soil can be effectively searched and quickly dealt with. The method is excellent for light sandy soils, and also for the normal woodland soils; it is less suitable for clay, and more difficult with peat soils, since so much of the latter material floats.

The larvae of the Tipulinae, being large, can be easily seen in spite of their dark colour, but although the Limoniinae are usually light in colour and the cuticle is washed clean, their smaller size is a disadvantage. The active Hexatomini can be seen readily, and these often pass through the mesh to the undersurface, so that it is better to sieve for only a short time before lifting the sieve out of the water to examine the underside. The more sluggish and the smaller larvae may not be visible, so as a general rule the detritus resulting from the sieving has been brought back indoors for subsequent treatment.

This preliminary sieving of the soil in the field has the great advantage of concentrating the larvae or pupae in a relatively small amount of detritus, and removes at least some of the suspended colouring matter present in all soils. The subsequent treatment may be either by using the flotation method or by simply searching the detritus in clean water.

In flotation, commercial magnesium sulphate, at the rate of about one pound per gallon of water, has been used, but this concentration can be varied, since it appears to differ in effectiveness in different types of soil. As a guide a few Hexatomine larvae previously removed from the detritus can be re-introduced; if these float the concentration is sufficient; if not more magnesium sulphate is added until they do. The larvae or pupae are removed immediately they are seen to clean water. The flotation method deals with most larvae and pupae but it is not satisfactory for the tube-living Limoniini, since the tubes of these larvae do not float.

The method, which has been used to obtain these tube-living larvae or pupae, is by repeated sieving indoors (using a 6″ or 8″ sieve of the same mesh) to remove all suspended matter, and then to examine the detritus systematically in clean water in a white dish. The larval tubes are then visible, and the larvae will extrude their anterior segments if left for a short time. This repeated sieving should be done with care since too prolonged sieving with its inevitable rather rough treatment will kill the larvae; the pupae are particularly susceptible in this respect.

Both repeated sieving and prolonged immersion in the magnesium sulphate solution will eventually bring the larvae and the pupae out of their tubes, but neither is recommended on account of the effects. Magnesium sulphate is used as a narcotic in some zoological techniques, and the larvae and pupae should be removed from this solution as soon as possible.

The flotation method can be used in the field, but it is cumbersome, and sieving has been found to be generally useful, particularly in taking samples. Soils, even those apparently identical, can vary greatly in the numbers of larvae found, and the soils vary at different times of the year. Spring of course is an excellent time. Quick sampling with a sieve can be done to estimate the richness of the various samples so that further investigations can be limited to those offering the best results.

The use of Orthodiehlorobenzene (Brindle, 1960) has not been thought suitable for the Limoniinae: though suitable for the Tipulinae, it is probably too drastie for the others.

For the larvae in habitats other than soil, the usual eolleeting methods have been used. The wood-feeding larvae are often only just below the surfaee so that a knife has been generally used to pare off thin sliees of wood to reveal the larval tunnels. More vigorous methods are neeessary if the larvae are deeper in the wood.

Searehing by hand appears to be best for moss-feeding larvae; shredding the moss over a sheet is sometimes effective espeeially with such larvae as *Diogma,* but the larvae tend to be so tangled with the moss that the shredding has to be thorough. Washing the moss in magnesium sulphate solution is sometimes effective, more espeeially with aquatie mosses to obtain such larvae and pupae as those of *Limonia didyma.*

Preservation

The larvae or pupae are first plaeed in elean eold water in order that the former will beeome active and fully expanded; they are then plaeed in hot (70° C) water which kills them immediately, and leaves them fully expanded. Aleohol-based killing fluids tend to make the larvae shrink, and do not kill them immediately. After immersion in hot water they are placed in Pampel's fluid for some time previous to storage in 70% aleohol. The initial use of Pampel's fluid seems to give eonsistently better results than when the specimens are plaeed direetly into aleohol, but sinee Pampel's fluid is unpleasant in use, storage in aleohol, whieh appears to be quite adequate, is mueh preferred. There has been no time limit observed for preservation in Pampel's, the larvae and pupae being removed to permanent storage in 70% aleohol when eonvenient.

Examination

Examination of the larvae or pupae has usually been made by using a binoeular microseope; the speeimens being placed in a small dish in alcohol for lateral viewing, and in a small wide tube for posterior viewing. The tube is filled with alcohol and loosely with cellulose wool, and an opening made down the centre of the wool, so that a larva can be inserted head downwards, with its anal segment just below the surfaee. A $\times 10$ or $\times 15$ lens is often quite sufficient for identification. Pupae are placed in the tube head upwards, and adjusted so that the pronotal horns can be seen from various angles.

The figures in the present paper have been drawn from larvae and pupae observed by the methods outlined, using a squared eye-piece. The magnification of the figures varies, but lengths have been given in the text for all larvae and pupae. The posterior views of the anal segments of the larvae represent a fully expanded

segment. The anal segments of the pupae are, unless otherwise stated, from a lateral view, dorsal side towards the top of the paper, and the rest of the pupa to the left. Only one side of the anal segment of the pupa is figured, the side towards the observer, so that if the anal segment has three pairs of dorsal spines, three single spines are figured. Any unpaired spines or protuberances along the mid-dorsal line are also shown. The positions from which figures of the pupa and pronotal horns have been drawn are described as ventral, dorsal, and lateral, these referring to the pupa itself, and not its position in relation to the vertical or horizontal; if the pupa is upright, a ventral view would correspond with an anterior view. The pronotal horns, unless otherwise stated, have been drawn from a more or less lateral view.

3. General

The larvae of the Tipulidae are prominent members of the soil fauna, especially that of marshy soils, and are partly conspicuous by their relatively large size, and partly by their activity. Crisp and Lloyd (1954) found that these larvae "form the most prominent component of the mud flat fauna, and show in a close association nearly all the remarkable adaptations that have developed in the family, a range of structures that is unequalled in the larvae of any other insect family. Great differences in structure are found in forms whose imaginal characters show close relationships and these involve not only secondary features, such as the respiratory mechanisms, but more fundamental structures such as the head capsule".

It is owing to this wide range of adaptive features that the genera of the larvae are so readily distinguished, but the wide range which may exist in one tribe makes a key to the four tribes of the Limoniinae very difficult to construct without a large number of exceptions and alternatives. Whilst there is a basic agreement between the types of larval structure and the taxonomic division of the adults into tribes, in all the latter there are larvae which would more easily be accommodated in other tribes on larval characters. *Ula* (Pediciini), for example, would be better included in the Hexatomini, whilst *Helius* (Limoniini) would also be better included in this tribe. These exceptions, however, are mainly due to convergence as a result of similar feeding habits, or of habitats, and the basic taxonomic arrangement appears to be sound.

The larvae of the Tipulidae, with one exception, are readily distinguished from all other Diptera larvae by being metapneustic (one pair of spiracles, and these on the anal segment) and by having a retractile head capsule. The exception is *Taphrophila* which is apneustic, but which agrees otherwise with the family characteristics.

The larvae are elongated, mainly whitish or yellow in colour, sometimes darker, usually cylindrical, and, in the carnivorous forms, extremely active. The herbivorous or detritus-feeding

larvae tend to be more sluggish, and this is shown in an exceptional form in the Cylindrotominae, the larvae of which are extremely sluggish in any movement. Most of the larvae are retractile to some degree, though this varies in extent. The cuticle is generally smooth, occasionally tuberculate or with processes, and the colour of the larvae is usually due to the colour and density of the body pubescence, but not in the Cylindrotominae, and certain other larvae. The body may have welts, and rarely (one genus only) pseudopods.

The anal segment is usually truncate posteriorly, and bears the anal lobes; the spiracles are prominent on the truncated end of the segment. The anal lobes can close over the truncated end of the segment and the spiracles, and they are normally so closed, when the larva is below the surface, but the lobes are widely opened when the larva comes to the surface in order to obtain air. This segment is extremely varied in structure and is very useful taxonomically. The anal papillae are placed ventrally on the anal segment and are not so visible from a posterior view as those of the Tipulinae.

The head and mouthparts of the larvae vary in structure. The generalised head capsule of the Tipulidae as a whole consists of a comparatively strongly sclerotised depressed structure, with one mid-ventral longitudinal opening and two dorsal longitudinal openings. The head is composed of three main sclerites, a single dorsal median sclerite, and two lateral sclerites which curve to form the lateral parts of the head both ventrally and dorsally; these two sclerites are termed the lateralia by Alexander (1920). This massive head capsule is characteristic of the Cylindrotominae and the Limoniini; it is rather less massive in the Pediciini, and in many Eriopterini and Hexatomini the rigid part of the head is reduced to six longitudinal bars—two dorsal, two lateral, and two ventral; a type of head capsule which is termed dissected.

Connecting the two lateral sclerites ventrally in the massive head capsule is a fused plate, the hypostome, which forms the floor of the mouth; in the dissected type of head the hypostome is either unsclerotised, or forms a bar connecting the longitudinal bars so as to allow expansion of the head whilst swallowing.

The mandibles are of two main types, and move in a lateral plane: the massive blunt-toothed mandibles of the detritus-feeding larvae, or those which feed on vegetable material, including decayed wood, and the narrow falciform mandibles of the carnivorous larvae. In one of these latter (*P. discicollis*) the mandibles consists of a broad base and a narrow apical part, the latter of which is movable on the base, and can be brought down to close on the base in the same manner that a blade of a pocket knife fits into its handle.

The pupae of the Tipulidae are exarate, and may be distinguished from all other exarate Diptera pupae by the combination of the following characters.

The antennal sheaths are long, usually reaching to or beyond the bases of the wing sheaths; they are not swollen basally; the pronotal horns are usually simple (except in *Taphrophila*) and may be either sessile or elongated; both horns are about equal in length, not greatly inequal as in the Ptychopteridae. The pupae never occur in dense white silk cocoons nor have the thorax "humped" as in some Mycetophilidae. Though the pupae of the Limoniini and Pediciini usually occur in silken tubes, these tubes are not dense or white, and are covered with detritus. The tarsal sheaths of the pupae are arranged side by side (fig. 85, TLS) and are not superimposed as in the Trichoceridae and Anisopodidae, whilst the ends of the tarsal sheaths almost always extend beyond the apices of the wing sheaths (fig. 85, WS), and do not end at or before the apices as in the Ceratopogonidae and Psychodidae.

The pupae are rather elongated, the eyes being usually prominent (fig. 85, E); in some the head bears spines, a feature which is more characteristic of the Eriopterini, although spines also occur on the head in *Hexatoma* (Hexatomini). The antennal sheaths curve around the head and, if long, lie along the upper part of the wing cases. Arising from the pronotum are a pair of spiracular processes, or pronotal horns, which vary widely in size and shape in the different pupae (fig. 85, PH). The leg sheaths vary in length, some, e.g. *Ula,* being very long; the sheaths of the coxae occupy most of the space between the upper part of the wing sheaths (fig. 85, LS) and the sheaths of the tibiae and tarsi lie side by side between the lower part of the wing sheaths; below the apices of the latter the tarsal sheaths are free (fig. 85, TLS).

The abdomen is parallel-sided, or almost so, usually more or less smooth except for welts; prominent marginal or other spines so typical of the Tipulinae, are only well developed in the Hexatomini. The anal segment, however, in almost all pupae, bears spines; it is more or less rounded in male pupae and tapering in female pupae.

The emergence of the adult is similar in general, or other material, features to that of the Tipulinae. The pupa emerges from the soil or the pupal tube by means of the abdominal welts or spines, until the anterior half is exposed, the posterior part remaining in the soil or tube or other material. The pupal skin splits along a median line from the head backwards, the leg sheaths are disarranged, and splits also occur ventro-laterally to the head. The adult emerges leaving the pupal skin with the posterior part embedded in the substratum or the tube.

4. Ecology

The identification of the larvae and pupae of the Cylindrotominae and Limoniinae is partially simplified by their differences in habitats. Of the Cylindrotominae, *Cylindrotoma* is distinct by reasons of its caterpillar-like life feeding openly on the leaves of marsh plants; *Diogma* occurs in terrestrial mosses; *Triogma* in

semi-aquatic mosses; and *Phalacrocera* in aquatic mosses. Although *Diogma* also does occur in semi-aquatic mosses, the ecological differences between the genera are often well defined. The rather unusual appearance of the last three larvae has been commented upon by various authors, and the curious processes on the body, together with the colour and the very sluggish nature of the larvae, combine effectively in concealing them amongst their food-plants.

The main habitats from where the larvae and pupae of the Limoniinae have been obtained during the present study are shown in Table 1. Of these habitats damp soil is that typical of woodlands; marshy soil is taken as that in which the water table lies close to but not at the surface; whilst saturated soil is taken as that in which the water table lies at or above the surface. Even though these divisions can only be approximate they are useful as a convenience. Soil or sand by the edges of rivers and streams is sometimes a sharply defined habitat. In some cases this arises because the larvae appear to live in the bed of the stream or river and migrate to the bank in order to pupate, as in *Hexatoma*. The larvae of *Elaeophila* are usually common in such a habitat in Spring, and these larvae have comparatively rarely occurred in marshy soil, even though the water content may be similar. *Dicranota* appears to be another genus which may be more aquatic in the larval stage, and become more terrestrial in order to pupate.

From Table 1, it is clear that the majority of the genera of the Hexatomini and Eriopterini occur in marshy soil, but there is a great difference between these larvae in their modifications to a life in wet or very wet conditions.

The larvae normally live below the surface, and the spiracular disc and spiracles are hidden since the anal lobes are closed over the disc. The larvae must come to the surface at times in order to obtain air; at these times the anal segment must be thrust above the surface and the anal lobes opened to allow the air free access to the spiracles. This proceeding is more difficult when the water table is at or above the surface.

This unfolding and folding of the anal lobes over the spiracular disc, and modifications to the anal lobes to aid in obtaining air, have been developed in an entirely different manner in the Hexatomini to that developed in the Eriopterini.

The Hexatomini show a great plasticity of structure with regard to the anal segment; this feature may be partially correlated with the fact that they are largely carnivorous and active, and need to make more visits to the surface as a result of their greater activity. In general their anal lobes appear to close over the spiracular disc from roughly a dorsal and ventral direction, the lateral lobes closing in from a dorsal or dorso-lateral direction, whilst the ventral lobes close in from a ventral direction.

TABLE 1
Usual habitats of the larvae of the Limoniinae

	in fungi	decayed wood	under bark	wood detritus	damp soil	marsh soil	soil by edges of rivers and streams	saturated soil	semi-aquatic or aquatic	hygropetricous	in haline habitats
Ula	×										
Limonia (Metalimnobia)	×										
Limonia (L. decemmaculata)	×										
Epiphragma		×									
Austrolimnophila		×									
Lipsothrix		×									
Gnophomyia			×								
Limonia dumetorum				×							
Molophilus				×							
Taphrophila									×		
Elliptera										×	
Dactylolabis										×	
Thaumastoptera						×					
Limonia					×	×			×		×
Helius						×		×	×		
Pedicia						×	×	×	×		
Trichyphona					×	×	×	×			
Dicranota						×	×	×	×		
Hexatoma							×				
Phylidorea						×	×	×			
Elaeophila							×				
Pseudolimnophila						×		×			
Pilaria, discicollis gp.						×	×	×			
Pilaria, nemoralis gp.					×	×	×	×			
Pilaria, filata gp.						×					
Oxydiscus						×					
Limnophila						×	×				
Gonomyia						×	×				
Cheilotrichia						×					
Erioptera						×	×	×			×
Ormosia						×					
Scleroprocta							×				
Rhypholophus						×	×				
Molophilus					×	×	×				

In this tribe the development appears to have been either in an increase in the length of the marginal hairs of the anal lobes, the four lobes remaining equal in size (fig. 56), or in an elongation of the ventral lobes only, with a very great increase in size of the length of the hairs on these lobes (fig. 59). These long ventral

hair fringes are very effective in holding the spiracular disc of the larva at the surface of water, and the larva can be freely suspended by this means. Such a suspension will also occur in preserved larvae in Pampel's fluid or 70% alcohol, at least for a short time. The effectiveness of the suspension is so great that the larva may have to curl over the spiracular disc in order to break the suspension (as shown in Lindner, 1959, p. 306, fig. 83).

The larvae of *Elaeophila* show a different development, in that all the four lobes are long and cylindrical, without long hair fringes (fig. 53, 54); these lobes can also be opened out. In these larvae a bubble of air can be held between the lobes when the larvae leave the surface.

It should be noted, however, that *Pseudolimnophila* shows the elongation of the ventral lobes particularly well and this larva is not carnivorous, though it is typical of very wet soils.

Whilst these modifications are evidently adaptations to a very wet environment, the absence of such modifications does not necessarily indicate a terrestrial larva. *Hexatoma* (fig. 38) shows few modifications, and yet it is semi-aquatic during much of its larval life. On the other hand the presence of such modifications does indicate that the larva is typical of very wet habitats.

In contrast to the Hexatomini, the Eriopterini show a much less diverse form; none have the anal segments greatly modified, and no development of long hair fringes occurs. The anal lobes of this tribe, as pointed out by Crisp and Lloyd (1954) appear to be able to fold down their mid-line in many larvae. This is possible because the dark sclerotised parts of the lobes are lateral in position, and there is usually a longitudinal unsclerotised line down the middle of the lobes. When the lobes close over the spiracular disc they close in a petaloid manner, and not from a dorsal and ventral direction as in the Hexatomini.

The Eriopterini are herbivorous, and much less active than the Hexatomini, which may partially account of the less highly modified anal segments, since their visits to the surface for air would seem to be much less often. In spite of their relatively unspecialised anal segments the Eriopterini have a wide range of habitats ranging from marshy soil to the sand in haline pools.

The larvae of the Limoniini, in general, appear to be the most generalised type, with a massive head capsule and with a simple anal segment, which shows little trace of anal lobes. Although many of the genus *Limonia* (sensu lato) live in damp woodland soil, some prefer much wetter habitats, for example the subgenus *Dicranomyia,* which ranges from woodland soil (*modesta*); semi-aquatic mosses (*mitis*), and mosses in running water (*didyma*), to submerged vegetation in haline pools near the coast (*ventralis*). Although the size of the spiracles in *ventralis* is much larger than those of many similar larvae found in woodland soils, the spiracles of *modesta* are equally large; *didyma* has small spiracles, whilst those of *unicolor* (marine algae) are still smaller.

It is clear that the size of the spiracles alone is of no significance in separating the aquatic larvae from the terrestrial larvae; the aquatic *Pedicia* has small spiracles, and a thorough comparative study of the respiratory mechanisms of the larvae of the Tipulidae as a whole would be extremely interesting.

Only three genera of the Limoniinae occur in decayed wood, feeding on the wood and forming larval tunnels, and none of these is as highly modified for such a life as, for example *Tanyptera* (Tipulinae). *Austrolimnophila* appears to be the most specialised, since it has very small anal lobes; both *Epiphragma* and *Lipsothrix* have prominent anal lobes. All of these occur often in dry hard wood but they also occur in much more rotten wood at times. *Gnophomyia* is the only larva normally found under relatively fresh bark of decaying trees: whilst *Limonia dumetorum* has been reported from decayed wood it may only be a detritus feeder and not a true wood-feeding larva; *Molophilus* also occurs in wood detritus or soil developed under old bark.

The fungus-feeding larvae seem to be confined to the three species of *Limonia* (*Metalimnobia*), and *Limonia* (*Dicranomyia*) *decemmaculata,* together with *Ula,* although other larvae of the genus *Limonia* may well occur in this material.

Thaumastoptera is unusual in living in a flattened elliptical case amongst mud near small woodland streams; the case is distinctive amongst the Tipulidae, although some Chironomidae build a rather similar shape of case.

Only two genera occur in hygropetricous habitats, in the sense of water flowing down vertical or inclined rock faces, presumably feeding on the algae or other vegetation which develops. *Elliptera* is possibly restricted to habitats where a good deal of splashing occurs; it also apparently takes advantage of artificial hygropetricous habitats, such as runways carrying water. *Dactylolabis* has only been obtained where a film of water was present.

Taphrophila is distinctive in living inside silken tubes covered with sand or detritus, built on submerged stones. The tubes are sinuous and tend to follow any cracks or inequalities of the stone: the pupae also remain in the tubes It seems possible that *Orimarga* may have a similar type of larva.

Although the pupae are often found in the larval habitats, some at least are more terrestrial than the larvae. If the larvae of *Phylidorea, Elaeophila* or *Hexatoma* are prevented from coming to drier soil to pupate they usually die without pupating; if such pupae are kept in saturated soils they also fail to produce adults. In rearing such larvae therefore provision has always been made so that the larvae can migrate to drier soils prior to pupation.

Under natural conditions, there is always the risk of the pupae of a marsh species being submerged, at least for a short time, and some pupae appear to be able to cope with sudden flooding. It will be noticed that in flotation there is a tendency for the pupae to collect around the edges of the water surface, at the junction

of the water with the sides of the dish, and some pupae, for example those of *Erioptera vicina* float readily in water. When soil containing such pupae is sieved, all the pupae immediately come to the surface, a feature which is likely to be valuable during flooding, the pupae being left on the surface of the soil when the water subsides. Hinton (1954) has drawn attention to the fact that the apical parts of the pronotal horns of *Pseudolimnophila* tend to bring the pupae to the edge of the water when the pupae are immersed.

In three genera or species-groups, the pronotal horns are very long, and since these pupae are those of species which inhabit very wet soils, or at least marshy soils, the elongation of the pronotal horn may be taken as adaptive to very wet conditions. The size and shape of the pronotal horns throughout the Limoniinae, however, are so variable that no simple explanation appears to be capable of covering all the modifications.

The larvae of *Phylidorea* and *Limonia* occur in different habitats, those of *Phylidorea* in marshy soil whilst *Limonia* is typical of drier soils. The pronotal horns of both are similar in being short and broad. This similarity may be partially explained by the fact that the larvae of *Phylidorea* tend to come to drier soils to pupate, so that the environment of the pupae would be similar.

Amongst the pupae which exist in aquatic habitats, however, a wide variation of pronotal horns exists. Those of *Limonia* (*G.*) *unicolor* (in marine algae) are very long; those of *Taprophila vitripennis* (running water) are many branched, and those of *Limonia* (*D.*) *didyma* (mosses in running water) are more or less short and simple.

The pronotal horns of two of the wood-feeding species of Limoniinae (*Epiphragma* and *Austrolimnophila*) are strongly curved; this is similar to those of the Tipulinae, in which the wood-feeding species have strongly curved pronotal horns or the horns are very short. In contrast, however, the third wood-feeding genus of the Limoniinae (*Lipsothrix*) has very large pronotal horns which form a cup-shaped structure, a form for which it is difficult to account.

The variety of form of the pronotal horns of the pupae of the Limoniinae is such that it would seem that a thorough comparative study of these structures would be extremely interesting, and could well be combined with a study of the respiratory mechanisms of the larvae as previously mentioned.

5. Larval Characters

Colour: the colour of the larva is useful in identification, although some variation does occur. The colour usually depends on the colour and density of the pubescence on the cuticle, but not in all cases. The colour of the larvae mentioned therefore may be due to the pubescence; if this is thick and dense, the pubescence may appear irideseent.

Welts: in the terrestrial larvae, locomotion is assisted by means of welts, which are transverse ridges situated near to the anterior margins of the abdominal segments. The welts may either be ventral or dorsal in position, and are often provided with small spines or spinules. The welts may not be protuberant, even though they are conspicuous, as in *Limonia* (fig. 13), but in the wood-feeding larvae they are very protuberant, as in *Lipsothrix* (fig. 65). In *Pedicia rivosa,* conical tubercles are developed at each end of the welts.

In the larvae which live in wetter habitats, especially those which occur in such unstable material as saturated sand or soil, the penultimate segment can be inflated, thus affording anchorage for the anal segments whilst the anterior segments are pushed forwards. Such inflation is characteristic of *Elaeophila, Hexatoma,* and other Hexatomini, and does occur in some Pediciini. In these larvae welts are usually absent or almost so. In only one genus, *Dicranota,* are true pseudopods present.

Anal segment: this is the most useful means of identification. The anal segment is usually truncate posteriorly and bears the two prominent spiracles. The central part of the truncate posterior surface around the spiracles is shining white and smooth, and is known as the spiracular disc (fig. 36 SD). This is covered with a secretion from the peri-spiracular glands (Keilin, 1913, 1944) which makes the disc hydrofuge, and this hydrofuge area may occupy only the centre of the posterior surface (as in figs. 42, 43) or it may extend on to the posterior surfaces of the anal lobes.

Around the spiracular disc are the anal lobes, four in the Cylindrotominae, and five or less in the Limoniinae. In the Cylindrotominae, the lobes consist of a pair of dorso-lateral lobes and a pair of ventro-lateral lobes (figs. 6, 8, 10, 12). In the Limoniinae, if five lobes are present (fig. 36) these consist of a dorsal lobe (DL), two lateral lobes (LL) and two ventral lobes (VL). In the Eriopterini there are typically five more or less equal lobes (as in fig. 74), but in the Hexatomini the dorsal lobe is usually reduced in size so that only four lobes are often prominent (fig. 56). There are only two ventral lobes in the Pediciini (figs. 32, 34), and the lobes are almost absent in the Limoniini (figs. 14-21). The anal lobes are usually flattened, but are cylindrical in the Pediciini, and in *Elaeophila* in the Hexatomini.

There are certain exceptions to the above: *Helius* (Limoniini) has five anal lobes (fig. 22) whilst *Ula* (Pediciini) also has five lobes (fig. 36). The larvae of *Pilaria* (*filata* group) in the Hexatomini, have the lobes apparently permanently closed, so that the anal segment appears to be conical (fig. 62). *Gonomyia* is unusual in the Eriopterini in having no prominent anal lobes, but the spiracular disc is distinctive in being very heavily pigmented (figs. 68-70).

The anal lobes have hairs along their margins, termed marginal hairs or hair fringes in the present paper: these hairs may be short or long; they may be of equal length (fig. 56) or the hairs on the ventral lobes may be greatly elongated (fig. 64). The finest range of this development occurs in the Hexatomini and forms a useful taxonomic character.

The spiracular disc may be entirely shining white, but often it bears dark patches: these patches giving attachment to muscles which can effect an infolding of the disc, according to Crisp and Lloyd (1954). The anal lobes are usually pigmented (=sclerotised) at least partially on the posterior surfaces, and the important feature for identification is that the position, size, and shape of the pigmented patches on the spiracular disc and on the posterior surfaces of the anal lobes are characteristic of a genus, and often of a species. These marks or patches are referred to in the text as pigmented spots, lines, or marks. As in the Tipulinae the constancy of these marks is remarkable. Although the characters based on these to separate *Ormosia, Erioptera* and *Molophilus* may seem tenuous, on known larvae they form a constant reliable character. Whether the other larvae of these genera, when known, will agree with the present characters is a matter for further study.

Anal Papillae: the larvae have four anal papillae around the anus, on the ventral surface of the anal segment (fig. 35, AP). As in the Tipulinae these are much smaller in the terrestrial larvae than in the more aquatic larvae. The former have four small rounded papillae, whereas in the latter the papillae are elongated. These papillae are retractile, and to observe them in an aquatic larva, the latter should be immersed in water. The form of these papillae is not used as a primary taxonomic character.

6. Pupal Characters

Colour: the colour of the pupae except when newly formed varies from mainly whitish to almost black. As a rule the pupae of the Limoniini are mainly white, but are yellow on the anal segment, and on the head, thorax, and thoracic appendages; those of the Pediciini are greyish or yellow, whilst those of the Eriopterini are whitish, grey, or yellow, usually darker anteriorly and on the anal segment. The Hexatomini pupae are mainly darker, except for the wood-feeding species. The head, thorax, and thoracic appendages of the lighter pupae turn black prior to emergence of the adult.

Welts or spines: The pupae of the Limoniini and Eriopterini have welts on some abdominal segments, both dorsally and ventrally; those of the Pediciini may lack well developed welts, or they may be dorso-lateral in position. The Hexatomini are the only tribe in which the abdominal segments, other than the anal, possess numerous spines.

Protnotal horns: the pupae are propneustic, with a pair of spiracular processes on the pronotum, situated posterior or slightly ventrad to the head (figs. 85, 86, PH). The spiracular processes are termed pronotal horns in the present paper. The size and shape of these horns varies a good deal, and the appearance of these can usually place a pupa to its genus, aided by the structure of the anal segment. They are probably almost as useful a character as the anal segment is in the larvae. The horns may be rather flattened or depressed as in *Pedicia* (fig. 94) but are usually more prominent and may be very elongated as in *Pseudolimnophila* (fig. 137). The spiracular openings mainly consist of small pores arranged in rows along the margin of the pronotal horn, but the horns may be extremely complex in structure. In the present paper the horns are regarded as taxonomic characters and only the external appearance is considered.

Anal segment: the structure of the anal segment separates the sexes of the pupae since that of the male is blunt, whilst that of the female is more or less acuminate. The latter is separated into the dorsal cerci sheaths (fig. 88, CS) and the ventral sheaths of the sternal valves (fig. 88, SVS). In *Gnophomyia* (fig. 143) the sheaths of the sternal valves are very small, whilst those of the cerci are extremely long. In *Gonomyia* (fig. 148) the cerci and sternal valve sheaths are equal in length.

The spines on the anal segment are best developed in the Hexatomini, but most pupae have at least one pair. There may be three pairs of dorsal spines (fig. 88), the antero-dorsal (AD), the medio-dorsal (MD), and the postero-dorsal (PD), together with one pair of anal spines (AS). In certain genera of the Eriopterini, the antero-dorsal spine is single, so that five dorsal spines are present. As a rule the anal spines of the male are much larger than those of the female; and in the latter the anal spines are on the cerci sheaths and may be very small.

Although lateral and ventral spines may occur, these are not developed to any marked extent generally, and little use has been made of these in the keys except where there are exceptional features.

Mesonotal spines, tubercles or setae: in the Epiopterini the mesonotum almost always has spines, tubercles, or setae developed on the posterior margin of the mesonotum (as figs. 147, 154, 158, etc.). This character is useful in separating most of the pupae of this tribe from those of the Hexatomini. One genus of the Eriopterini, however, may have one or more of these features, so that these features are of less value in separating genera. All known *Molophilus* pupae have strong spines (including those of American species figured in Alexander, 1920). In *Ormosia* either setae or spines may be present; in *Gonomyia* there are either spines or tubercles; whilst in *Erioptera* there may be setae or spines. There seems to be a gradation from very strong and closely packed setae to spine-like processes.

The spines or setae are directed backwards, and the spines which are flattened and thorn-like, usually have their longer axis vertical (as fig. 173); in some, however (fig. 159) the spines are depressed, whilst in *Scleroprocta* (fig. 154) the mesonotum has a wide blackened ridge bearing numerous very short spinules.

7. Key to subfamilies

The subfamilies of the Tipulidae may be distinguished in the immature stages as follows: —

Larvae

1. Spiracular disc with six lobes, the lobes flattened or cylindrical, sometimes reduced in size, rarely entirely sclerotised ..... Tipulinae
— Spiracular disc with five or fewer lobes 2
2. Body with prominent processes in longitudinal rows, the processes at least as long as half width of body ..... Cylindrotominae
— Body smooth, without prominent processes; if the cuticle is tuberculate the tubercles are much less than half width of body ..... Limoniinae

Pupae

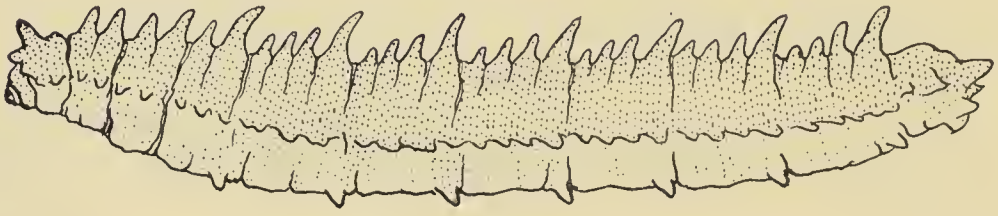
1. Sheaths of maxillary palpi recurved at apices; pupae larger with rows of small spines near posterior margins of abdominal segments ..... Tipulinae
— Sheaths of maxillary palpi not recurved at apices; pupae usually smaller, with or without spines 2
2. Pupae either with pairs of long spines on abdominal segments, at least on sixth and eighth tergites, or pupae free and attached to stems of phanerogamic plants ..... Cylindrotominae
— Pupae without pairs of long spines, and never attached to stems of phanerogamic plants ..... Limoniinae

8. Cylindrotominae

Four species in four genera are recorded from Britain, the larvae and pupae of all being easily recognised. The larvae, except for that of *Cylindrotoma,* are very unusual in appearance, having long filiform or smaller toothed processes in rows along the body. That of *Cylindrotoma* is unique in living freely on phanerogamic plants. Lenz (1920b) has described the immature stages of all the species, and Wesenberg-Lund (1943) gives some details of their biology. Hemmingsen (1952, 1960) has published excellent accounts of the oviposition in *Diogma, Phalacrocera,* and *Cylindrotoma.* Brauns (1954a, 1954b) has figured the larvae and pupae of all except *Phalacrocera.*

The eggs are laid on moss, or on higher plants (*Cylindrotoma*) and the cerci of the female move alternately and parallel to each other during oviposition, but only in *Cylindrotoma* does this

result in a slit being cut in the leaf edge, in which an egg is placed. In the other genera the eggs are attached to the mosses by lateral adhesive portions, those of *Phalacrocera* being developed as club-shaped structures.



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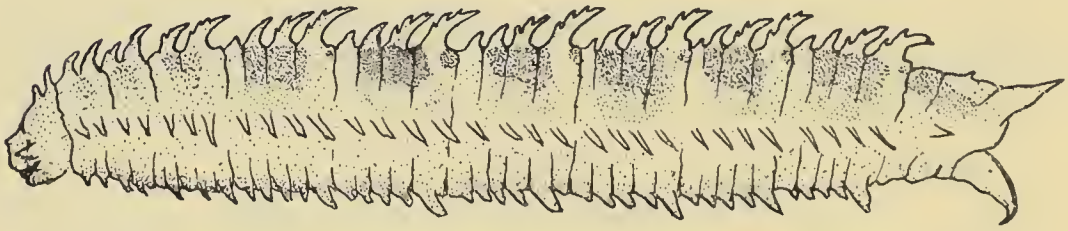

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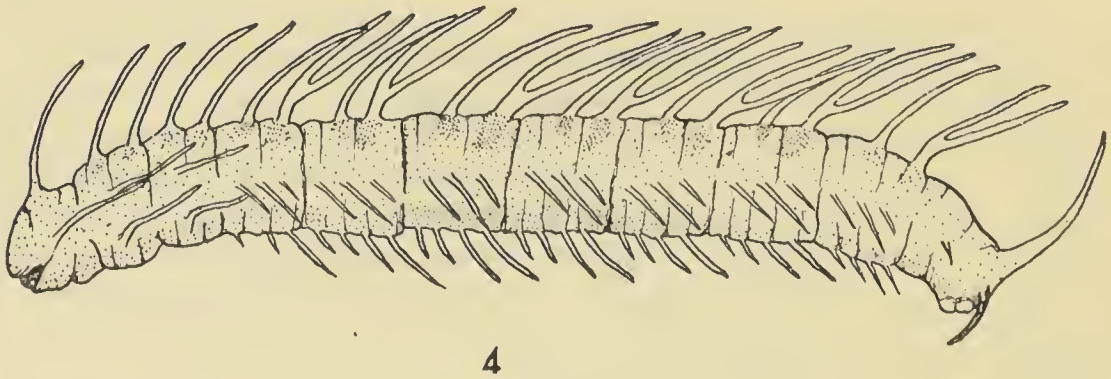

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Cylindrotominae

FIGS. 1-4.—Larvae (lateral)—1, *C. distinctissima*; 2, *T. trisulcata*; 3, *D. glabrata*; 4, *P. replicata*.

Key to larvae

1. Dorsal processes toothed on anterior convex side 2
— Dorsal processes not toothed 3
2. Dorsal processes with three or more teeth on anterior side (fig. 2); brown, in semi-aquatic mosses ..... *Triogma*
— Dorsal processes with two or fewer teeth on anterior side (fig. 3); green, usually in terrestrial mosses ..... *Diogma*
3. Dorsal processes in a double row, long and filiform, some being bifid (fig. 4); in aquatic mosses ..... *Phalacrocera*
— Dorsal processes in a single row, short and tuberculate (fig. 1); on phanerogamic plants ..... *Cylindrotoma*

Key to pupae

1. Basal abdominal tergites without long spines 2
— Basal abdominal tergites with long spines 3
2. Distal abdominal segments with long spines; pronotal horns long (fig. 5); aquatic ..... *Phalacrocera*
— Distal abdominal segments without spines; pronotal horns short (fig. 11); on terrestrial plants ..... *Cylindrotoma*
3. Anal segment with long spines directed posteriorly; each tergite with three pairs of spines (fig. 9); in semi-aquatic mosses ..... *Triogma*
— Anal segment with long spines directed dorsad; each tergite with one pair of spines (fig. 7); in terrestrial mosses ... *Diogma*

Cylindrotoma Macquart

Larvae free living on the leaves of *Caltha, Viola, Stellaria, Anemone, Petasites,* and *Chrysosplenium,* in marshy woodland habitats. Light green, darker dorsally, with rows of small tubercles along the body (fig. 1). Posterior spiracles dorsal in position, no obvious spiracular disc (fig. 12). Length: 20 mm.

Pupae yellowish-white or greenish, mesonotum with small flap-like processes (fig. 11); hanging head downwards from plants, the cast larval skin retained at base of pupa. Length: 15 mm.
One species, widely distributed ..... *distinctissima* Meigen

Diogma Edwards

Larvae usually in terrestrial mosses growing on stones in limestone woodlands, less often in wet mosses growing on soil. Green, with brown or blackish markings, and with distinctive toothed processes along the body (fig. 3); anal segment with posterior spiracles inside cavity, each ventral lobe with a broad brown or blackish band, the bands lighter medially and at the bases (fig. 8). Length: 18 mm.

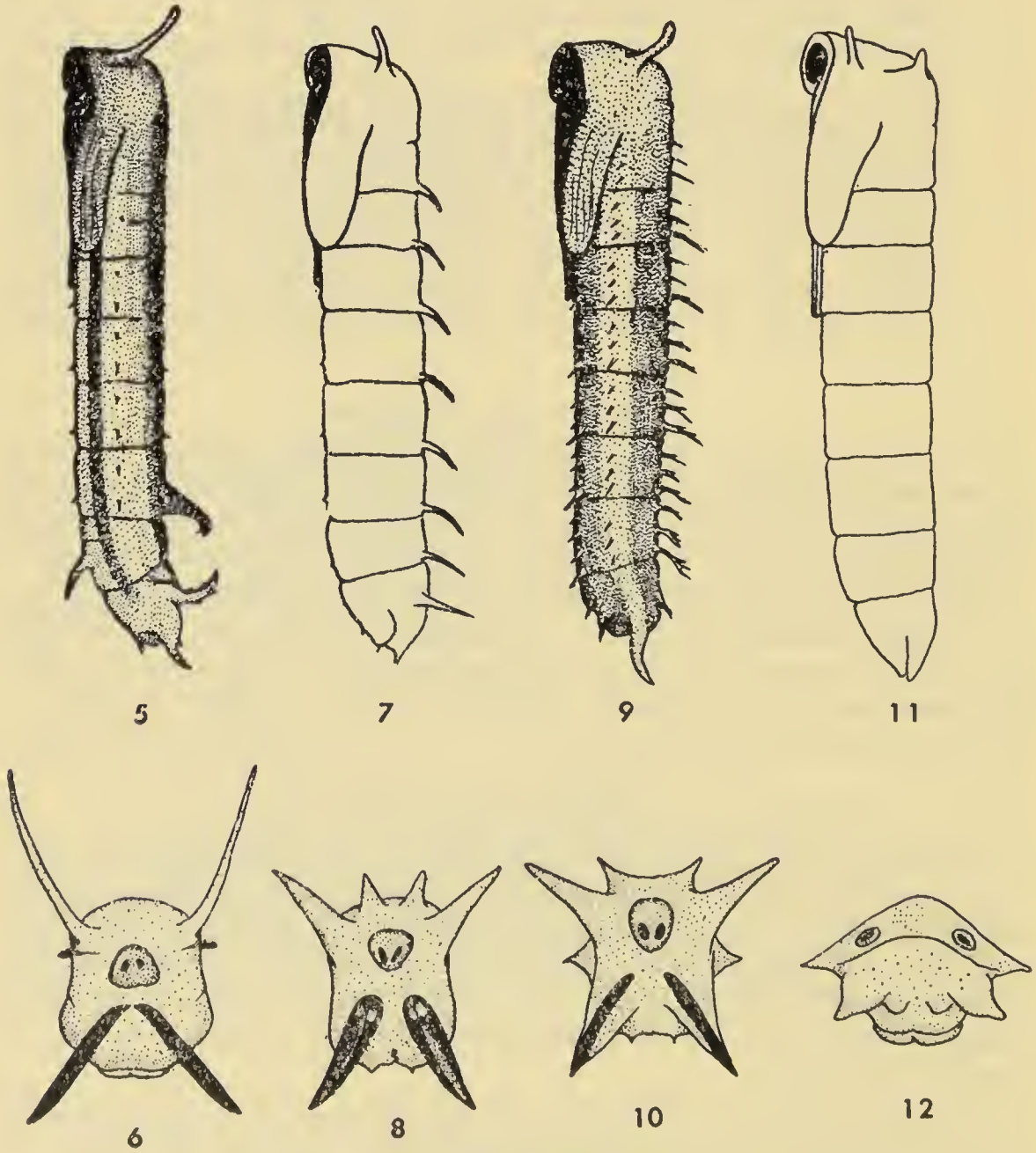
Pupae greenish, variegated with darker markings, amongst the mosses; tergites with one pair of long spines on each, placed towards posterior border (fig. 7). Length: 15 mm.
One species, local but not uncommon ..... *glabrata* Meigen

Triogma Schiner

Larvae in semi-aquatic mosses on moors, e.g. *Hypnum cuspidatum*. Dark brown or brownish-green, lighter ventrally, and with darker markings along dorsum; rows of toothed processes along body (fig. 2); anal segment with posterior spiracles inside cavity, each ventral lobe with a narrow black line (fig. 10). Length: 20 mm.

Pupae dark brown anteriorly, abdomen lighter with dark stripes; amongst the mosses; each tergite with three pairs of spines, the tips of which are "frayed", posterior spines longer than anterior ones (fig. 9). Length: 15 mm.

One species, locally common ..... *trisulcata* Schummel



Cylindrotominae

FIGS. 5-12.—Pupae (lateral) and anal segments of larvae (posterior)—5, 6, *P. revlicata*; 7, 8, *D. glabrata*; 9, 10, *T. trisulcata*; 11, 12, *C. distinctissima*.

Phalacrocera Schiner

Larvae in aquatic mosses in acid pools, on moors or in woodlands, e.g. *Hypnum fluitans* or *Sphagnum*. Dark brown or lighter dorsally, whitish ventrally and between the segments; distinctive long filiform appendages along the body (fig. 4); anal segment with posterior spiracles inside cavity, ventral lobes entirely blackish posteriorly (fig. 6). Length: 25 mm.

Pupae amongst the mosses, with the tips of the pronotal horns reaching the surface of the water. Dark brown anteriorly, the abdomen whitish with dark stripes, pronotal horn very long (fig. 5). Length: 15 mm.

One species, locally common ..... *replicata* (Linnaeus)

Miall and Shelford (1897) give details of the internal and external structure of the larva.

9. Limoniinae

Alexander (1920), Crisp and Lloyd (1954) and Lindner (1959) should be consulted for the biology and structure of the larvae of this subfamily. Lindner (1958a) gives an account of the eggs of this subfamily.

The larvae and pupae can be approximately separated into tribes as follows: —

Larvae

1. Herbivorous, in silken tubes, no obvious anal lobes ..... Limoniini
2. Carnivorous, free-living, two anal lobes ..... Pediciini
3. Carnivorous, free-living, four anal lobes ..... Hexatomini
4. Herbivorous, free-living, five anal lobes ..... Eriopterini

Pupae

1. In silken tubes, abdomen whitish ..... Limoniini
2. In silken tubes, yellowish or grey ..... Pediciini
3. Free, abdomen spinous; mesonotum simple ..... Hexatomini
4. Free, abdomen not spinous; mesonotum with spines, setae or tubercles ..... Eriopterini

There are, however, a number of exceptions to the above, since not all the Limoniini live in silken tubes as larvae, and not all those of the Hexatomini are carnivorous, whilst the latter usually have a fifth dorsal anal lobe though this is much reduced in size. Some of the Eriopterini have only four anal lobes.

Due to the genera whose larval and pupal characters do not agree with the more typical larvae and pupae of their tribe, it is only possible to give an adequate key to the tribes by using a number of exceptions and alternatives, a method which tends to make a key difficult to use. The more practical method is to give a key to genera, arranged irrespective of the tribes, and this is the type of key in the present paper. After the key to larvae and key to

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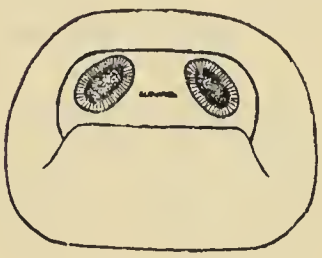

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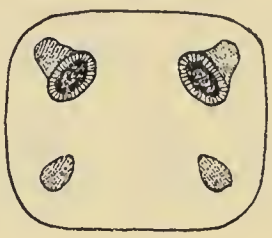

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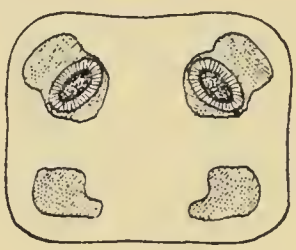

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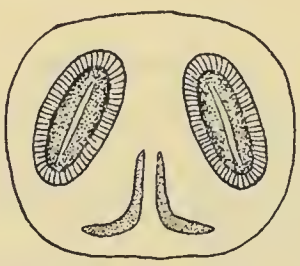

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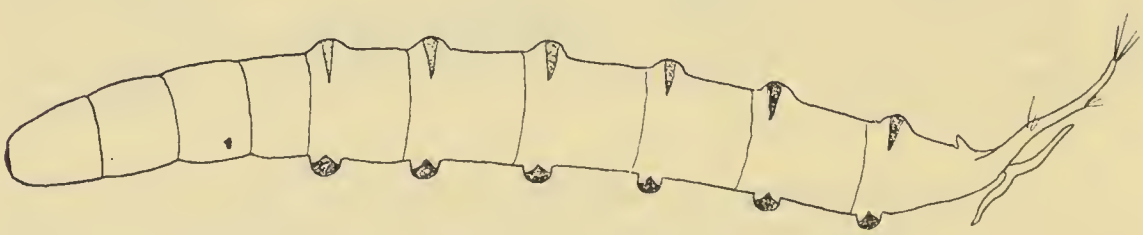

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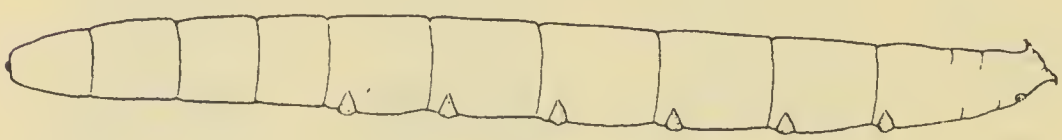

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Limoniini (larvae)

FIGS. 13-24.—Larvae (lateral)—13, *L. bifasciata*; 23, *T. vitripennis*; 24, *H. longirostris*. Anal segments (posterior) or spiracular discs—14, *L. bifasciata*; 15, *L. nubeculosa*; 16, *L. macrostigma*; 17, *L. decemmaculata*; 18, *L. ventralis*; 19, *L. didyma*; 20, *L. mitis*; 21, *L. maculata*; 22, *H. longirostris*.

pupae a short description of the genera, sub-genera, and species-groups follows, arranged in tribes according to Coe (1950) and to the check list given on p. 213.

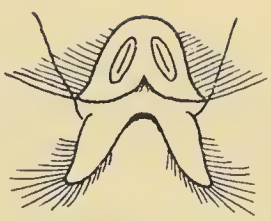
The larva and pupa of *Rhabdomastix schistacea* (Schummel) were described by Beling (1886) but there are not sufficient details given to enable either the larvae or pupa to be included in the present paper. The pupa has spines on the mesonotum, and thus agrees with other Eriopterine pupae.

Gerbig (1913) described the larvae of *Erioptera* (*Trimicra*) *pilipes* (Fabricius) in some detail. The anal segment has five nearly equal anal lobes which are blackened on the posterior surfaces. According to these details the larva would run down to couplet 26 in the larval key and be confused with that of *Scleroprocta*. However the anal lobes of the latter are black on both surfaces and the margins are finely dentated; in *pilipes* the anal lobes are only black on the posterior surfaces and are not finely dentated on the margins. The larva of *pilipes* is discussed further under *Erioptera*.

Bangerter (1929) describes the larva and pupa of *Orimargula alpigena* Mik, which are remarkably like those of *Taphrophila vitripennis*. Although *Orimargula alpigena* is not on the British List, two species of *Orimarga* occur in Britain. This latter genus was listed in a group containing *Taphrophila* and *Orimargula* by Alexander (1920), so it is possible that the larvae and pupae of *Orimarga* may be similar to those of *Taphrophila*.

Key to larvae

1. Larvae in a hardened greatly flattened elliptical case (fig. 27); white or greenish-white, with thoracic segments hairy; anal segment emarginate dorsally with short dark marginal hairs (fig. 28); in marshy soils near small woodland streams *Thaumastoptera*
— Larvae not in a hardened flattened elliptical case 2
2. Anal segment with two cylindrical or tapering lobes (figs. 23, 32, 34) 3
— Anal segment without such lobes, either with 4 or 5 flattened lobes (cylindrical only in *Elaeophila*) or without obvious lobes 6
3. Spiracles absent; dorsal and ventral welts prominent; anal lobes very long (fig. 23) and angular when seen from a dorsal view, in silken tubes on stones in flowing water ..... *Taphrophila*
— Spiracles present and prominent on anal segment; not in silken tubes 4
4. Anal lobes short, spiracular disc large (fig. 34); four ventral welts not developed as tubercles or as pseudopods (fig. 30); yellowish or whitish; in damp or marshy soils *Trichyphona*
— Anal lobes longer, spiracular disc small (fig. 32); four or five pairs of welts, tubercles or pseudopods 5



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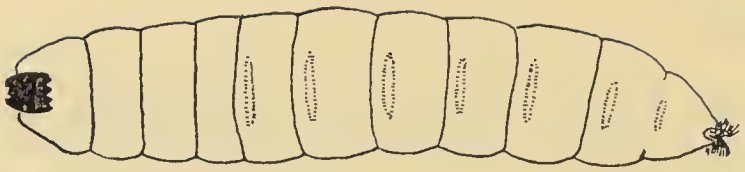

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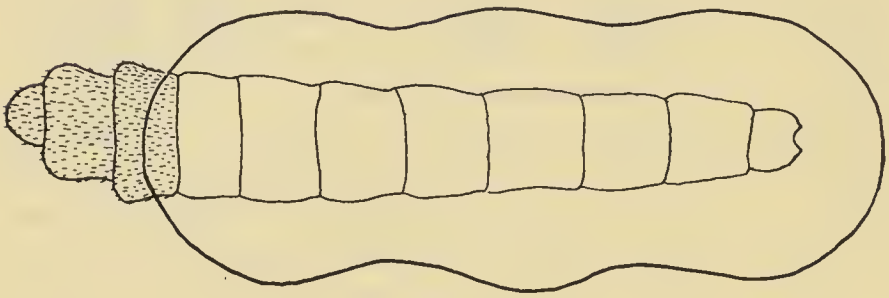

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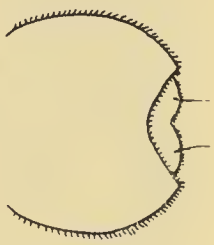

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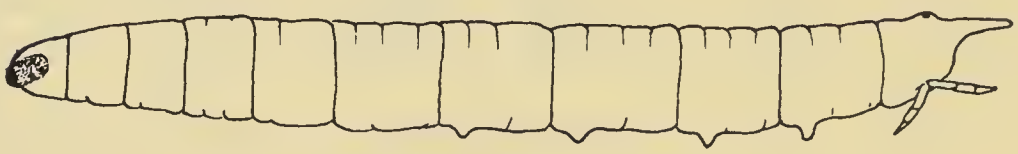

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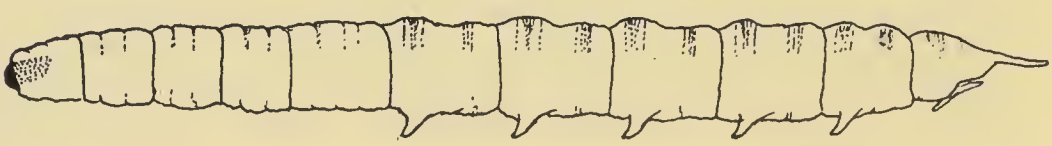

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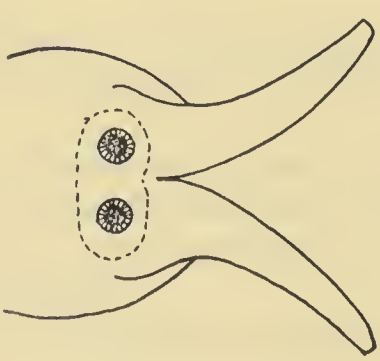

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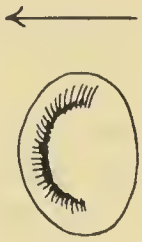

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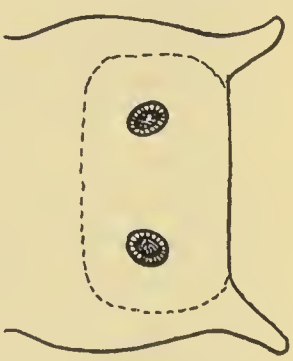

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Limoniini (larvae)

FIGS. 25-28.—*E. omissa*—25, anal segment; 26, larva, dorsal (from Alexander (1920) after Mik (1886)). *T. calceata*—27, larva, dorsal (outline shows larval case); 28, anal segment, dorsal.

Pediciini (larvae)

FIGS. 29-34.—29, *P. rivosa*; 30, *T. immaculata*; 31, *D. robusta* (all lateral). Anal segments, dorsal—32, *D. robusta*; 34, *T. immaculata*. Tip of pseudopod—33, *D. robusta* (arrow shows anterior direction).

5. Pseudopods well developed, in five pairs ventrally (fig. 31), each pseudopod with prominent circular rows of small hook-like spines on the tip (fig. 33); cuticle with short dark hairs, usually showing transverse banding; in aquatic mosses, or in marshy soils near streams and rivers ..... *Dicranota*
— Four pairs of welts or tubercles (fig. 29) which have no ventral hook-like spines; cuticle with lighter hairs, often sparse, without or with only slight transverse bands; colour either white, yellow, or light brown; freely aquatic, in aquatic or semi-aquatic mosses, or in marshy soils ..... *Pedicia*

6. Larvae without prominent anal lobes; spiracular disc never heavily marked with black (figs. 14-21, 41) 7
— Larvae with four or five anal lobes, or with spiracular disc heavily marked with black (as figs. 67-70) 9

7. Anal segment conical, with tuft of long apical hairs (fig. 62); whitish, in marshy soils ..... *Pilaria* (*filata* group)
— Anal segment truncate 8

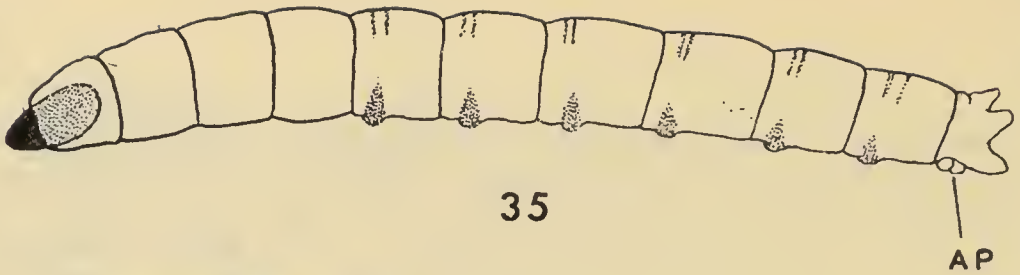
8. Ventral welts forming protuberances (as fig. 39); no prominent dorsal welts; spiracular disc pigmented as fig. 41; yellowish-white, in decayed wood, not in a silken tube ..... *Austrolimnophila*
— Ventral welts prominent but not protuberant as a rule; dorsal welts conspicuous (fig. 13); whitish, in silken tubes in soil, fungi, very rotten wood, or in semi-aquatic, or aquatic mosses, or aquatic plants; spiracular disc not pigmented as fig. 41, sometimes entirely shining white (figs. 14-21) ..... *Limonia*

9. Larvae inside the dead wood of trees or branches, feeding on the wood and forming larval tunnels 10
— Larvae not inside the dead wood of trees or branches and forming larval tunnels 11

10. Anal lobes not pigmented posteriorly (fig. 40); ventral welts conspicuous, dorsal welts absent or almost so (fig. 39); shorter and broader, yellowish-white ..... *Epiphragma*
— Anal lobes pigmented on posterior surfaces (fig. 66); ventral and dorsal welts conspicuous (fig. 65); longer and more slender, yellowish-white ..... *Lipsothrix*

11. Anal segment with four lobes, or with a reduced fifth dorsal lobe, the latter usually not, or hardly pigmented, except *Helius* (fig. 22); spiracular disc never mainly black (mostly Hexatomini) (figs. 22, 24, 25, 26, 37, 38, 42-64) 12
— Anal segment with five lobes always pigmented, the dorsal lobe often as large as the other lobes, or almost so, and pigmented; if lobes are indistinct, then spiracular disc mainly black (most Eriopterini) (figs. 36, 67-77) 22

12. Larvae short and broad, with a roughened or tuberculate cuticle; usually hygropetricous 13
— Larvae narrower and more elongated, usually with a smooth cuticle; not hygropetricous 14



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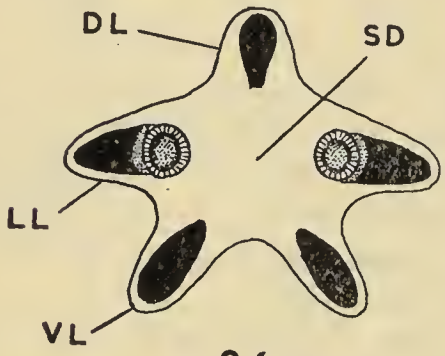

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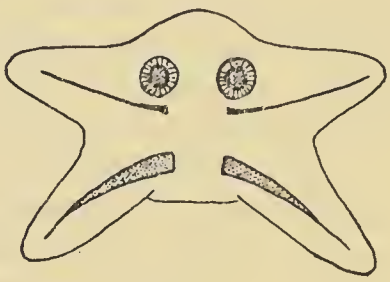

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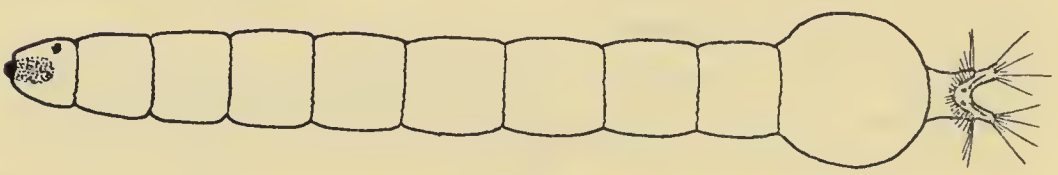

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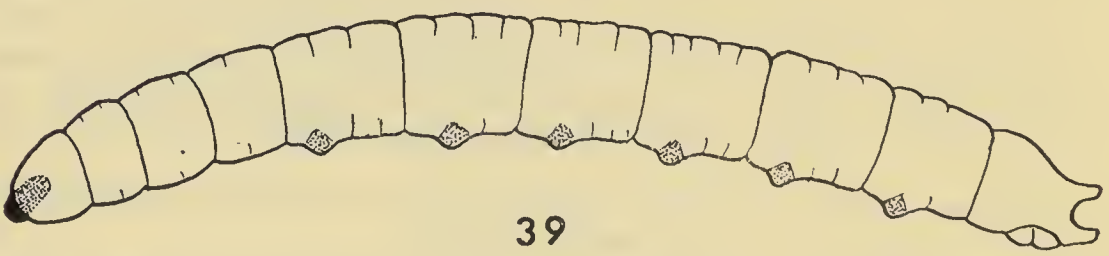

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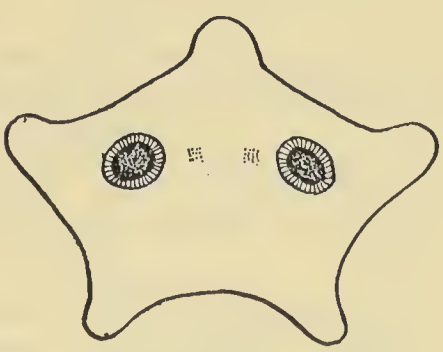

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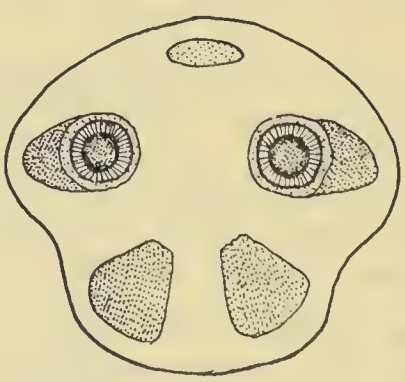

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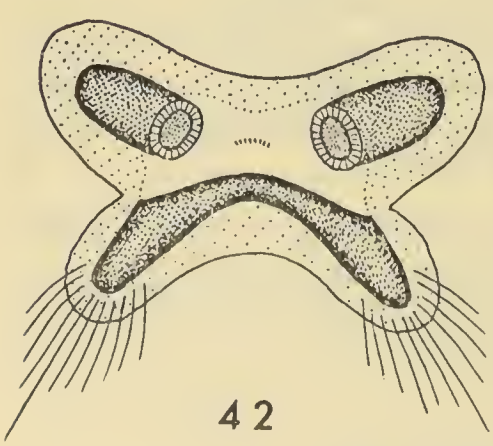

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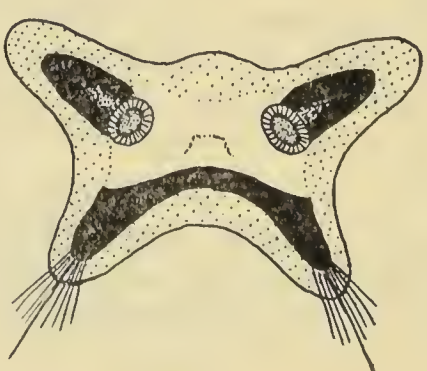

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For legend—see opposite page

13. Lateral anal lobes fringed with long hairs; spiracles elliptical (fig. 25); larvae (fig. 26) usually in elongated silken shelters on rocks or other supports in flowing water; greenish without darker markings ..... *Elliptera*
— Lateral anal lobes without long hair fringes; spiracles almost circular (figs. 42, 43); larvae yellowish or greenish, with darker markings; not in silken shelters ..... *Dactylolabis*
14. Lateral and ventral anal lobes subequal in size; marginal hair fringe of lobes not conspicuously longer on ventral lobes 15
— Lateral anal lobes shorter than ventral lobes; marginal hair fringe usually much longer on ventral than on lateral lobes 19
15. Lateral and ventral anal lobes forming long cylindrical processes (figs. 53, 54), the cuticle of which is covered with sparse dark pubescence; whitish in colour, rather darkened by the pubescence; mainly in soil or sand by the edges of rivers and streams ..... *Elaeophila*
— Lateral and ventral anal lobes flattened, not cylindrical ... 16
16. Lateral anal lobes with prominent hair fringes which are more extensive than those on ventral lobes (fig. 38); spiracular disc and lobes pigmented as fig. 37; greenish or brownish-green in colour; in sand by edges of rivers and streams ..... *Hexatoma*
— Lateral and ventral anal lobes with hair fringes all of approximately equal length; yellow or dark brown in colour 17
17. Anal lobes almost uniformly yellow on posterior surfaces, darkened apically; hair fringes very long, much longer than width of lobes at bases (figs. 55, 56); anal papillae elongated at tips (fig. 57); yellow or yellowish-brown, rather iridescent; in sand by edges of rivers or streams, or in marshy soils ..... *Limnophila* s.s.
— Anal lobes with darker borders, not uniformly yellow; marginal hairs much shorter than width of lobes at bases 18
18. Dorsal anal lobe prominent, though smaller than the other lobes, all lobes narrower and with narrow sharply defined dark borders (fig. 22); spiracular disc directed postero-dorsally (fig. 24); cuticle with very dense dark-brown or brown pubescence; in marshy soils, in sphagnum, or between the basal leaves of marsh plants ..... *Helius*

Pediciini (larvae)

FIGS. 35-36.—*U. sylvatica*—35, larva, lateral; 36, anal segment (posterior) (AP=anal papillae; SD=spiracular disc; DL=dorsal lobe; LL=lateral lobe; VL=ventral lobe).

Hexatomini (larvae)

FIGS. 37-43.—38, *H. bicolor* (dorsal); 39, *E. ocellaris* (lateral). Anal segments (posterior)—37, *H. bicolor;* 40, *E. ocellaris*; 41, *A. ochracea*; 42, *D. sexmaculata*; 43, *D. transversa.*

— Dorsal anal lobe smaller, all lobes broad, with dark, ill-defined borders (fig. 63); spiracular disc directed posteriorly; cuticle with yellow pubescence; in marshy soils ..... *Pilaria* (*nemoralis* group)

19. Ventral anal lobes very long, almost parallel-sided, both lateral and ventral lobes black posteriorly (fig. 61); hair fringes of anal segment very long; anal papillae as long as ventral lobes (fig. 60); in marshy or saturated soils ..... *Pseudolimnophila*

— Ventral lobes shorter, not parallel-sided; anal papillae shorter 20

20. Ventral anal lobes long, with most of surface darkened (fig. 59); anal papillae elongated (fig. 58); in marshy soils ..... *Pilaria* (*discicollis* group)

— Ventral lobes not so pigmented; anal papillae more or less rounded 21

21. Anal lobes with very long marginal hairs; spiracular disc and anal lobes pigmented as fig. 64; in marshy soils; smaller, 10 mm. or less ..... *Oxydiscus*

— Anal lobes with shorter marginal hairs; spiracular disc and lobes pigmented as figs. 44-52; in marshy soils; larger, at least 13 mm. ..... *Phylidorea*

22. Larvae short and broad (fig. 35); spiracular disc and anal lobes pigmented as fig. 36; in fungi ..... *Ula*

— Longer and more slender larvae; spiracular disc and anal lobes not so pigmented; not in fungi 23

23. Under bark of decaying trees; spiracular disc and anal lobes pigmented as fig. 67; whitish ..... *Gnophomyia*

— Not under bark of decaying trees; spiracular disc and lobes pigmented otherwise 24

24. Anal lobes short, inconspicuous; spiracular disc heavily pigmented with black (figs. 68-70); in sand or soil by edges of rivers and streams or in marshy soils ..... *Gonomyia*

— Anal lobes longer, conspicuous; spiracular disc and lobes not so heavily pigmented 25

25. The five anal lobes equal in size and pigmentation 26

— Dorsal lobe rather shorter than the lateral or ventral lobes and often not similar in pigmentation 27

26. All lobes blackish, with serrated or dentated margins (fig. 77); marginal hair fringe not well developed; whitish; in marshy soils near streams ..... *Scleroprocta*

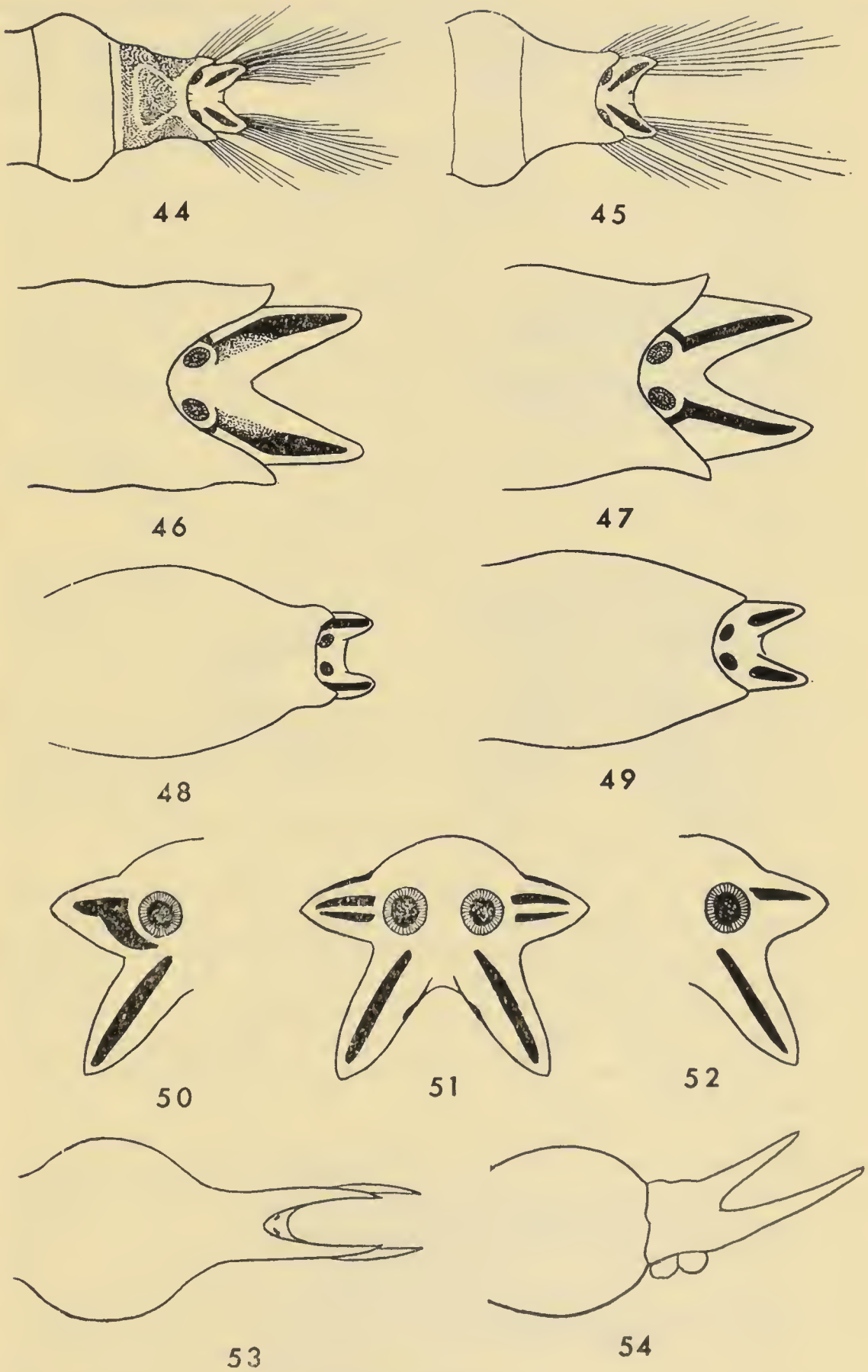
— Lobes dark brown, with well developed hair fringes (fig. 73); cuticle covered with dense dark pubescence; amongst wet leaves in gullies, or in marshy soils ..... *Rhypholophus*

27. Pigmented patch on lateral lobes not divided (fig. 71); in marshy soils ..... *Cheilotrichia*

— Pigmented patch on lateral lobes divided medially 28

28. No pigmented spot to the inner side of the spiracles (fig. 72); yellowish-white; in marshy soils ..... *Ormosia*

— A pigmented spot to the inner side of the spiracles 29



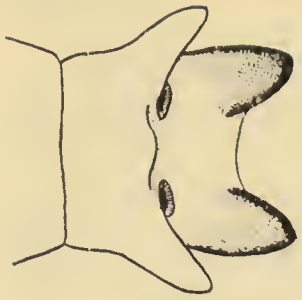
Hexatomini (larvae)

FIGS. 44-54.—Anal segments, dorsal—44, *P. meigeni*; 45, *P. lineola*; 46, *P. fulvonervosa*; 47, *P. ferruginea*; 48, *P. squalens*; 49, *I. pulchella*; 53, *E. maculata*; lateral—54, *E. maculata*; posterior—50, *P. lineola*; 51, *P. abdominalis*; 52, *P. squalens*. (Marginal hairs only shown in 44, 45.)

29. Larger, comparatively much broader larvae; pigmented spot on dorsal lobe divided medially (figs. 75, 76) ..... *Erioptera*
— Smaller, and more slender larvae; pigmented spot on dorsal lobe entire (fig. 74) ..... *Molophilus*

Key to pupae

1. Pupae enclosed within a hardened case or softer silken tube; abdominal segments whitish or yellow, with or without abdominal welts, never spinous; mesonotum without setae, spines or tubercles (most Limoniini and Pediciini) 2
— Pupae free; abdominal segments whitish or grey, or pupae uniformly yellowish brown, dark brown or blackish; abdominal segments with welts or with spines; mesonotum with or without setae, spines or tubercles (mostly Hexatomini and Eriopterini) 8
2. Case hardened, elliptical, flattened (fig. 27); pronotal horns long and curved; leg sheaths long (fig. 85) ... *Thaumastoptera*
— Case not hardened, but of silk with added material 3
3. Case elliptical; in hygropetricous habitats; pronotal horns large, broadened basally, narrowed distally, with finely dentated margins (figs. 86-87) ..... *Elliptera*
— Case tubular; not in hygropetricous habitats; pronotal horns otherwise 4
4. Pronotal horns characteristic, many branched (fig. 90); anal segments with one pair of spines, those of male (fig. 91) larger than those of female (as fig. 92); in silken tubes on stones in flowing water ..... *Taphrophila*
— Pronotal horns not many branched; pupae not in silken tubes on stones in flowing water 5
5. Pronotal horns usually short and broad; if elongated then the base is much broadened (figs. 78-84, 93); pupae with well developed welts, at least five abdominal segments with both dorsal and ventral welts ..... *Limonia*
— Pronotal horns either depressed, or narrowed at base, with or without a stem (figs. 94, 101, 103); pupae with dorsal and ventral welts on at most four abdominal segments, or welts dorso-lateral in position 6
6. Pronotal horns depressed, with dorsal sinuate opening (figs. 94, 96, 97); welts present dorsally and ventrally; pleurae of abdomen with dark striations (fig. 94); larger, probably always larger than 15 mm in length ..... *Pedicia*
— Pronotal horns not depressed, but erect and more or less flattened antero-posteriorly; pleurae of abdomen without dark striations; smaller, always less than 12 mm in length 7
7. Welts developed as short dark transverse bars on dorso-lateral parts of abdomen; pronotal horns with distinct stem (fig. 103) ..... *Dicranota*
— Welts not well developed, and dorsal or ventral in position; pronotal horns sessile (fig. 101) ..... *Trichyphona*



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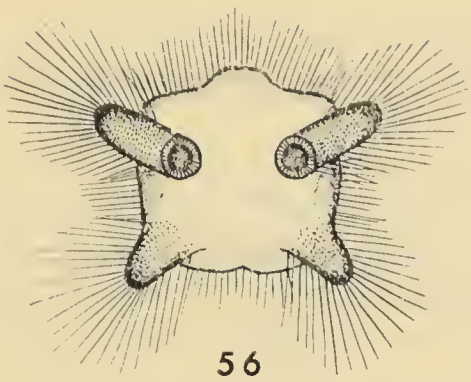

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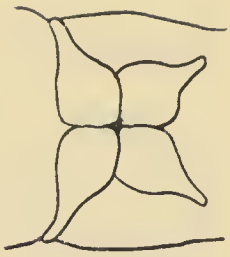

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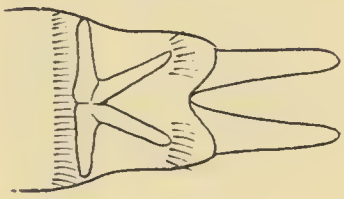

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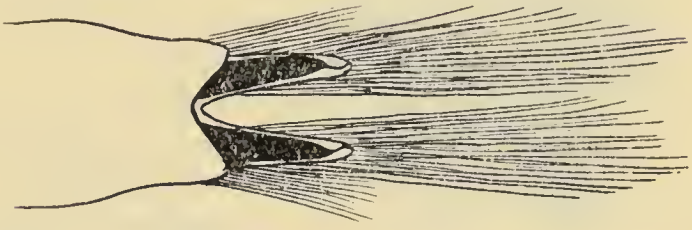

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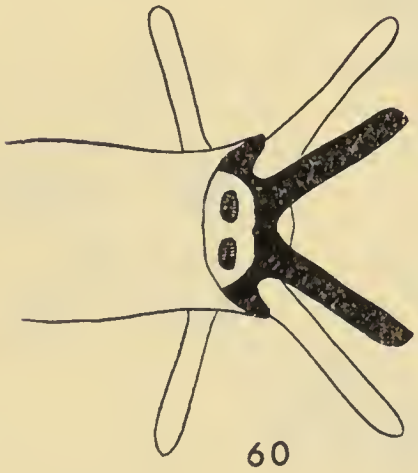

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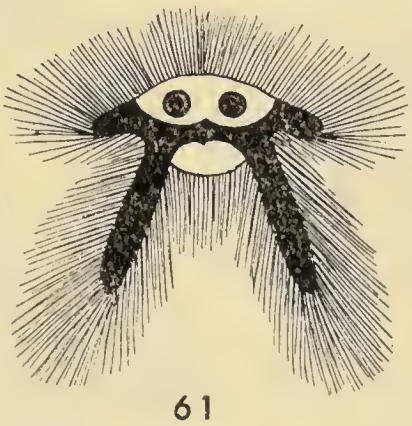

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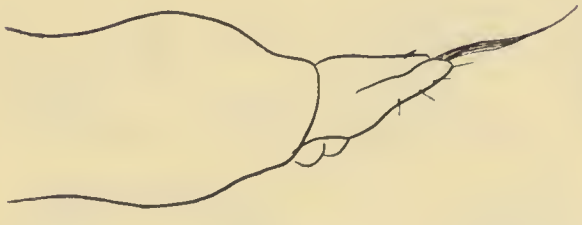

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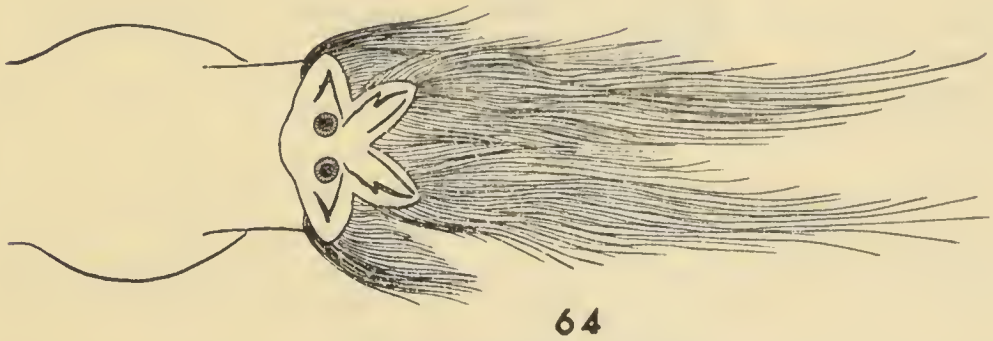

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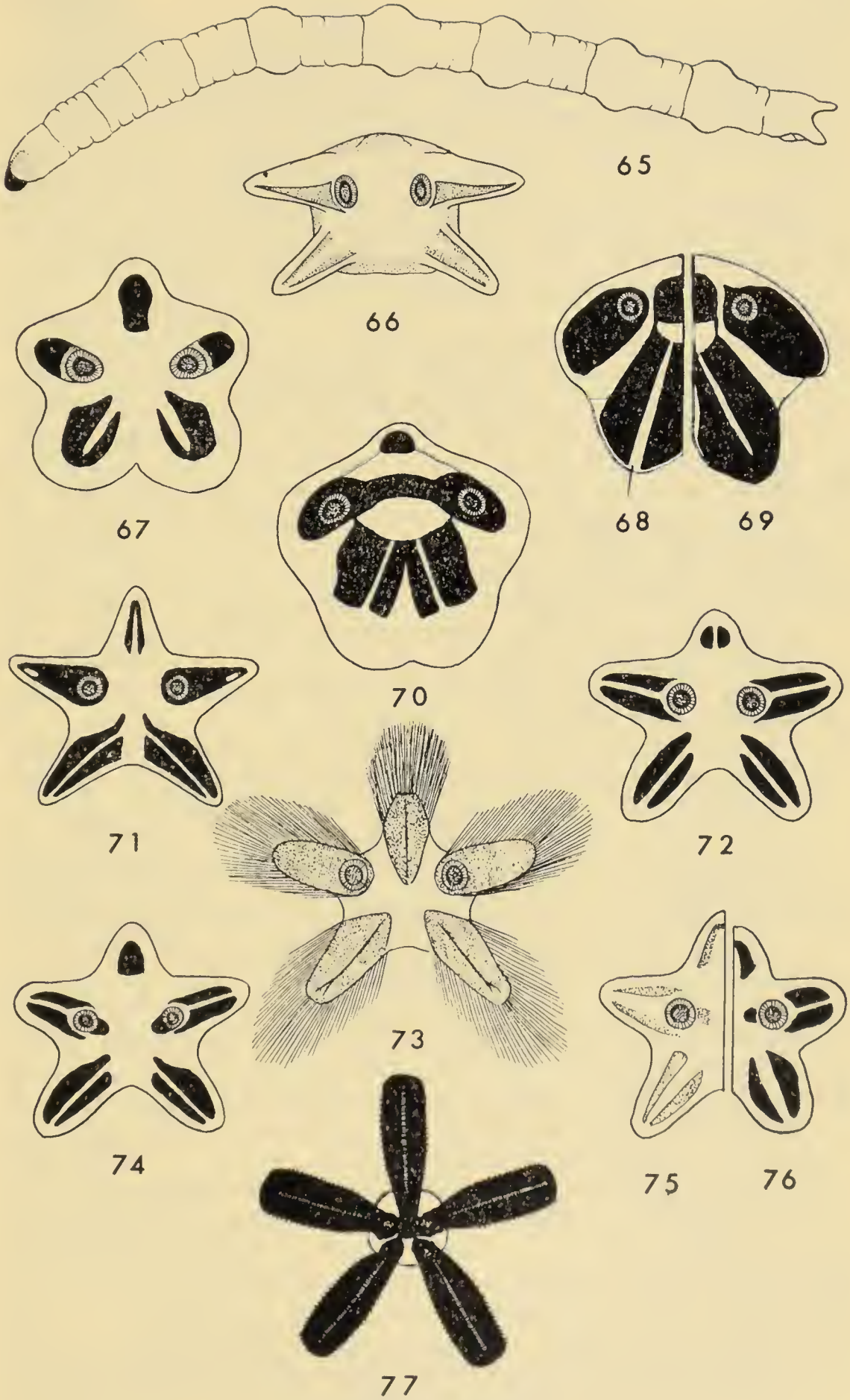
Hexatomini (larvae)

FIGS. 55-64.—Anal segments—55, 56, 57, *L. punctata* (dorsal, posterior, ventral); 58, 59, *P. discicollis* (ventral, dorsal); 60, 61, *P. lucorum* (dorsal, posterior); 62, *P. batava* (lateral); 63, *P. nemoralis* (posterior); 64, *O. senilis* (dorsal) (dorsal marginal setae omitted). (Marginal hairs only shown in 56, 59, 61, 62, 64.)

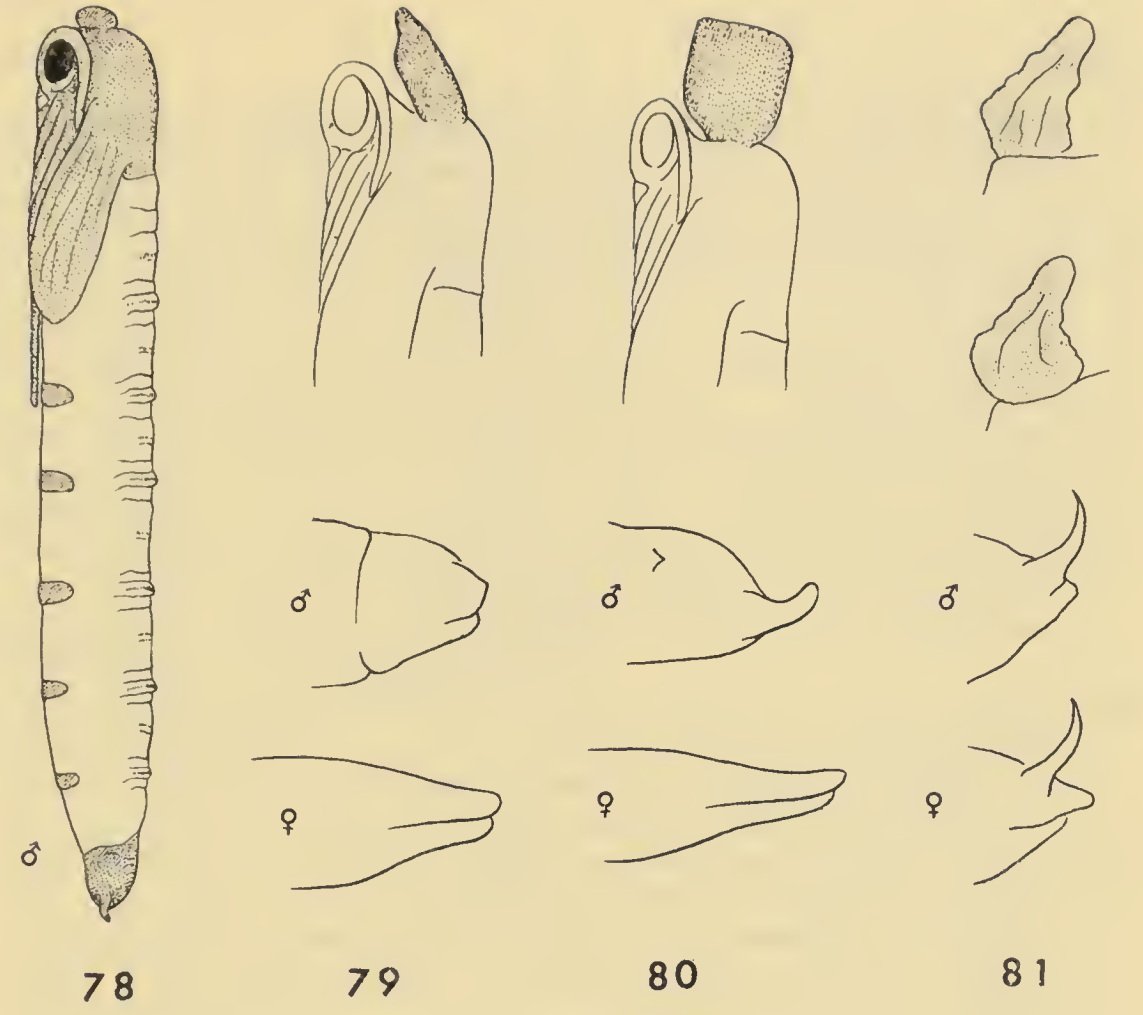
8. In moss in running water; pronotal horns either as fig. 81 ..... *Limonia didyma*
   or as fig. 103 ..... *Dicranota*
— Not in moss in running water; pronotal horns otherwise ... 9
9. Pronotal horns long, straight, diverging, tapered at apices (figs. 98, 99); leg sheaths very long (fig. 98); in fungi ... *Ula*
— Pronotal horns not so formed; not in fungi 10
10. Inside decayed wood of trees or branches; pronotal horns either strongly curved, without dilated or flattened apices, or very large and cup-shaped 11
— Not inside decayed wood of trees or branches; pronotal horns usually not curved or if so with dilated apices or pupae about 4 mm in length; pronotal horns never cup-shaped 13
11. Pronotal horns characteristic, cup-shaped (figs. 140, 142), the cup being formed by the two pronotal horns ..... *Lipsothrix*
— Pronotal horns long and strongly curved 12
12. Pronotal horns dilated at base (fig. 112); larger, 12 mm in length ..... *Epiphragma*
— Pronotal horns not dilated at base (fig. 110); smaller, 10 mm or less in length ..... *Austrolimnophila*
13. In hygropetricous habitats; pupae attached to last larval skin which is attached to substratum; cuticle of pupae tuberculate; pronotal horns elongated (figs. 107, 108) ..... *Dactylolabis*
— Not in hygropetricous habitats; pupae not attached to last larval skin; pronotal horns otherwise 14
14. Pronotal horns broad basally, triangular in shape (fig. 144); anal segments as fig. 143, that of female with very long cerci sheaths and almost aborted sheaths of sternal valves; under bark of decaying trees ..... *Gnophomyia*
— Pronotal horns and anal segments otherwise; not under bark of decaying trees 15
15. Mesonotum simple; yellowish-brown to blackish, abdomen not lighter in colour; pupae over 7 mm in length 16
— Mesonotum with spines, setae, or tubercles, or pupa under 5 mm in length; yellow or brown, abdomen often lighter in colour 25
16. Pronotal horns very long, about as long as wing sheaths (figs. 129, 131, 133, 137) 17
— Pronotal horns shorter, much shorter than wing cases ... 19
17. Pronotal horns with angular apices (fig. 131); abdominal segments with numerous spines (fig. 129); anal segment with tuberculate spines (fig. 130) ..... *Pilaria* (*discicollis* group)
— Pronotal horns rounded at apices (figs. 133, 137); abdomen with less numerous spines; anal segments without tuberculate spines 18

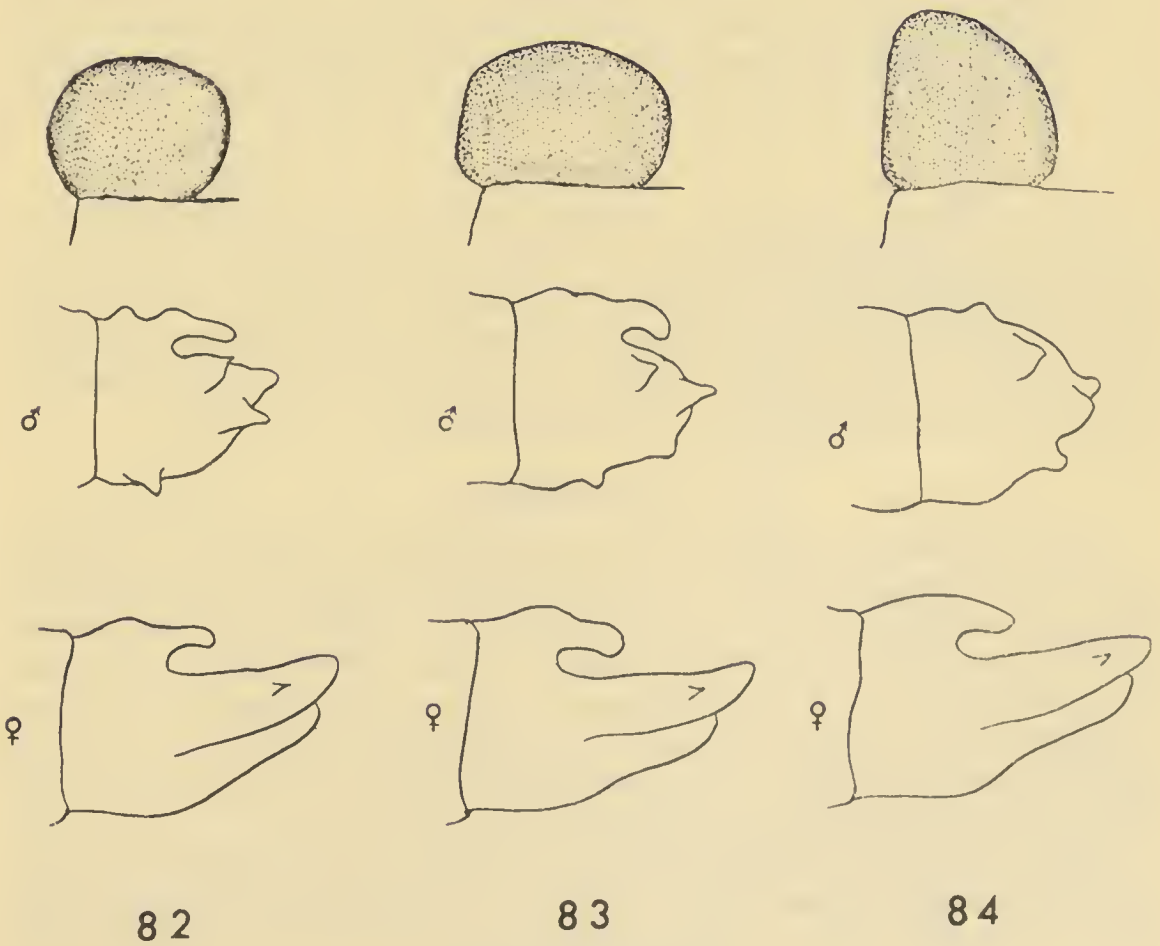


Eriopterini (larvae)

FIGS. 65-77.—65, *L. errans*, lateral. Anal segments, posterior—66, *L. errans*; 67, *Gn. lugubris*; 68, *G. lateralis*; 69, *G. alboscutellata*; 70, *G. lucidula*; 71, *C. cinerascens*; 72, *O. lineata*; 73, *R. haemorrhoidalis*; 74, *M. obscurus*; 75, *E. lutea*; 76, *E. vicina*; 77, *S. danica*. (68, 69, after Bangerter, 1928, 1930.)

18. Pronotal horns spatulate at tip (fig. 133); anal segments without prominent ridges bearing numerous long hairs; sternal valve sheath of female relatively longer (figs. 132, 134); pupae smaller, 10 mm in length or less ..... *Pilaria* (*filata* group)
— Pronotal horns with two flap-like processes at apices (fig. 137); anal segments with prominent ridges bearing numerous hairs (figs. 135, 136); sternal valve sheath of female relatively shorter; pupae larger, at least 11 mm in length ..... *Pseudolimnophila*
19. Abdominal segments, except for the anal, without spines; anal segments with prominent spines (fig. 88); pronotal horns elongated, dilated towards apices (fig. 89) ..... *Helius*
— Abdominal segments with spines; anal segment and pronotal horns otherwise 20
20. Head with prominent hook-like spines, one pair being on vertex (fig. 104); pronotal horns elongated not dilated at apices (fig. 105) ..... *Hexatoma*
— Head without such spines on vertex 21
21. Pupae smaller, length 7 mm or less; dorsal spines on anal segment truncate (fig. 138); pronotal horns elongate, with apices lighter in colour (fig. 139) ..... *Oxydiscus*
— Pupae larger, at least 9 mm in length; dorsal spines on anal segment not truncate 22
22. Pronotal horns broad, rather short, with apex almost truncate, not broadened basally, with sinuous apical opening (figs. 118, 119); pupae larger, 17 mm in length ..... *Limnophila* s.s.
— Pronotal horns otherwise; pupae smaller; at most 15 mm in length 23
23. Pronotal horns narrow, elongated, with distal third lighter in colour (fig. 114); anal segments (fig. 115); sternal valve sheath of female not pointed apically ..... *Pilaria* (*nemoralis* group)
— Pronotal horns broader; sternal valve sheath of female pointed apically 24
24. Pronotal horns broad, rather flattened laterally with prominent lighter apical third; apex not symmetrical when viewed laterally (fig. 128) ..... *Elaeophila*
— Pronotal horns broad, usually short, flattened laterally without prominent lighter apical part; apex symmetrical (figs. 122-126) ..... *Phylidorea*
25. Pupae smaller, under 5 mm in length 26
— Pupae larger, at least 7 mm in length 27
26. Mesonotum without prominent spines (fig. 150); pronotal horns shorter and straight (fig. 151); anal segments with two or three pairs of spines (fig. 152) ..... *Cheilotrichia*
— Mesonotum with prominent spines (fig. 173); pronotal horns longer and curved (fig. 173); anal segments with at most one pair of spines (fig. 172) ..... *Molophilus*





Limoniini (pupae)

FIGS. 78-84.—78, *L. bifasciata*, lateral. Pronotal horns and anal segments of—79, *L. decemmaculata*; 80, *L. ventralis*; 81, *L. didyma*; 82, *L. nubeculosa*; 83, *L. macrostigma*; 84, *L. tripunctata*.

27. Pronotal horns short and broad, with or without a stem (figs. 145, 146, 149); mesonotum with spines (fig. 147) or tubercles; anal segment with small spines (fig. 148) ..... *Gonomyia*
— Pronotal horns elongated, not short and broad 28
28. Anal segments with only one pair of spines or none (figs. 155, 162, 167) 29
— Anal segments with at least two pairs of spines (figs. 156, 157, 161, 170) 30
29. Pronotal horn constricted at base (fig. 153); mesonotum with blackish transverse ridge bearing numerous very short spinules (fig. 154) ..... *Scleroprocta*
— Pronotal horn not constricted at base (figs. 163, 166, 168); mesonotum with single large spines and setae (fig. 165); smaller spines; or short stout setae (fig. 164) ..... *Erioptera* (*Erioptera* s.s. and *Symplecta*)
30. Anal segment with short spines (fig. 170); pronotal horn very long, dilated basally (fig. 171) ..... *Erioptera* (*Ilisia*)
— Anal segment with long spines (figs. 161, 157); pronotal horn less elongated, base dilated or not (figs. 158, 160) 31
31. Mesonotum with depressed spines (fig. 159); pronotal horn longer and rather dilated basally (fig. 160); spines on anal segment broadened and cuticle blackened around bases of spines, the single anterodorsal spine represented by a blackened tubercle (fig. 161) ..... *Rhypholophus*
— Mesonotum with short setae (fig. 158) or vertical spines; pronotal horn shorter, not dilated basally (fig. 158); spines on anal segment long and narrow, fleshy or sclerotised, without blackened bases; the single anterodorsal spine similar to the other dorsal spines in shape (figs. 156, 157) ... *Ormosia*

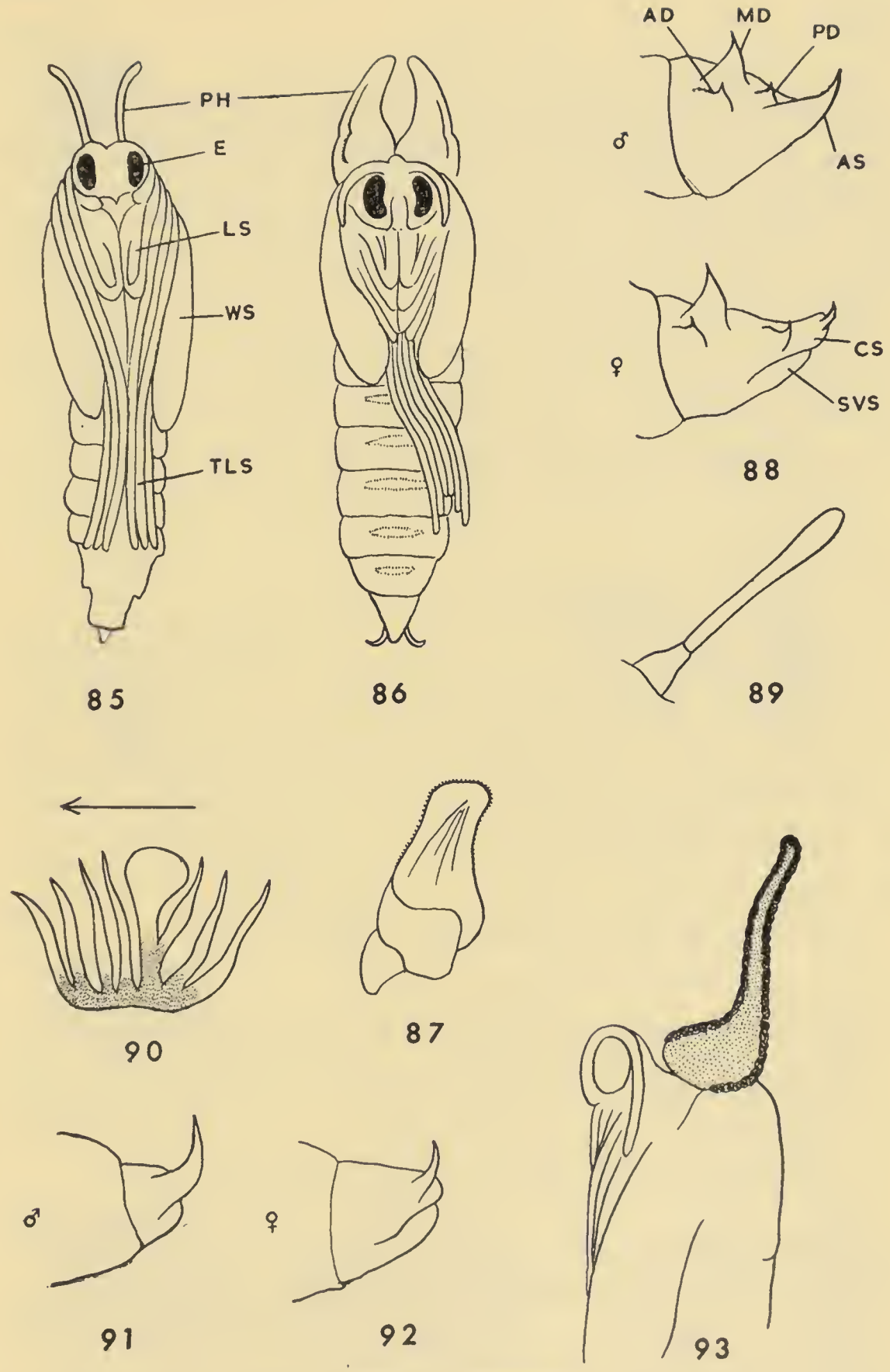
Limoniini

The tribe is dominated by the large genus *Limonia,* with its subgenera, all showing many features in common. *Helius* is exceptional in many respects. The larva and pupa of *Limonia* (*Discobola*) *annulata* (Linnaeus) is apparently unknown, so that the sub-genus *Discobola,* of which *annulata* is the sole representative, is not dealt with in the present paper.

Limonia Meigen

The larvae and pupae of the subgenera of *Limonia* (*Limonia* s.s., *Dicranomyia* Stephens, *Metalimnobia* Matsumura, *Rhipidia* Meigen, and *Geranomyia* Haliday) are not sufficiently distinctive to be regarded as separate groups. It is a large genus, and only about one-quarter of the larvae and pupae are known. Lindner (1958b) gives an excellent account of the life history of *Limonia quadrinotata* Meigen, whilst Saunders (1930) deals with the life-history of *Geranomyia unicolor* Haliday.

The larvae are usually whitish, and the anal segment has no prominent anal lobes. Both dorsal and ventral welts are present, but not usually protuberant (fig. 13). There are four anal papillae,



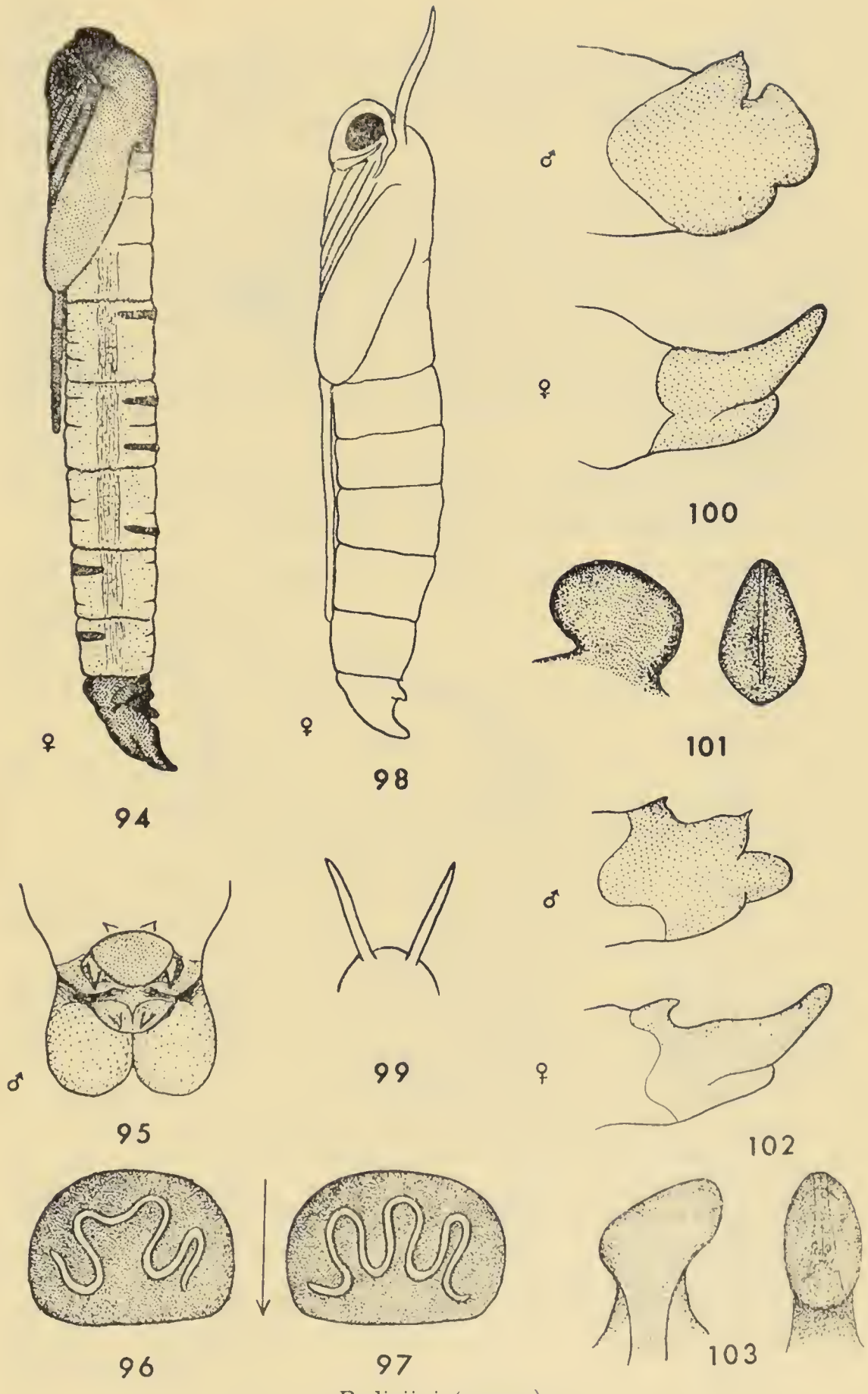
Limoniini (pupae)

FIGS. 85-93.—85, *T. calceata,* ventral (after Lenz, 1920); 86, 87, *E. omissa,* pupa ventral and pronotal horn (after Alexander, 1920); 88, 89, *H. longirostris,* anal segments and pronotal horn; 90, 91, *T. vitripennis,* pronotal horn, and anal segment (arrow shows ventral direction). 92, 93, *L.* (*G.*) *unicolor,* anal segment, and pronotal horn. (PH=pronotal horn; E=eye; LS=coxal sheaths; WS=wing sheath; TLS=sheaths of tarsi; AD=antero-dorsal spine; MD=medio-dorsal spine; PD=postero-dorsal spine; AS=anal spine; CS=cerci sheaths; SVS=sheaths of sternal valves.)

mainly small and rounded, but elongated in the more aquatic larvae. The larvae are herbivorous or detritus feeders, and live inside silken or gelatinous tubes, the exterior of which is covered with detritus. The larva of *L. didyma* is rather darkened, and the ventral welts are more pronounced: this larva does not live inside a silken tube, a feature which may be correlated with its life in mosses in running water. Length: 22-24 mm (*Metalimnobia*); 10-15 mm (others).

The known larvae can be partially separated into species by the pattern of pigmentation on the spiracular disc, or the absence of such pigmentation. A provisional key is given below: —

1. Spiracular disc unpigmented or almost so (figs. 14, 19) ... 2
— Spiracular disc with distinct pigmented spots (figs. 15-18, 20-21) 5
2. Aquatic 3
— In fungi (*Metalimnobia*) 4
3. Spiracular disc smaller, marginal hairs short but strong; in marine algae ..... *unicolor* (Haliday)
— Spiracular disc larger (fig. 19); marginal hairs short but fine; in moss in fresh running water ..... *didyma* Meigen
4. A dark line between spiracles; no dark spot on ventral part of spiracular disc (fig. 14) ..... *bifasciata* Schrank
— No dark line between spiracles; a dark spot on each side of ventral part of spiracular disc ..... *quadrinotata* Meigen
quadrimaculata Linnaeus
5. Pigmented spots confined to area below and touching spiracles (fig. 21); in dung or in compost heaps .....
maculata Meigen
— Pigmented spots otherwise 6
6. Spiracles of normal size (figs. 15-17, 20); pigment in more or less rounded spots or marks 7
— Spiracles very large (fig. 18); pigment in L-shaped or triangular marks 11
7. Two pigmented spots only, placed on the lower part of spiracular disc (fig. 20); in semi-aquatic habitats .....
mitis Meigen
— Four pigmented spots 8
8. Upper spots not touching spiracles (fig. 17); in fungi .....
decemmaculata Loew
— Upper spots touching spiracles; in woodland soils 9
9. Spots larger, upper spots rather quadrangular (fig. 16) .....
macrostigma Schummel
— Spots smaller and rounded (fig. 15) 10
10. Spiracular disc as fig. 15 ..... *nubeculosa* Meigen
— Spiracular disc with dorsal spots rather larger, ventral spots more elongated ..... *tripunctata* Fabricius
flavipes Fabricius



Pediciini (pupae)

FIGS. 94-103.—94, 95, 96, 97, *P. rivosa*, pupa, lateral, anal segment dorsal, and pronotal horns, from above (=anterior) (arrow shows ventral direction); 98, 99, *U. sylvatica*, pupa, lateral and pronotal horns, dorsal; 100, 101, *T. immaculata*, anal segments, and pronotal horn, lateral and ventral; 102, 103, *D. robusta*, anal segments, and pronotal horns, dorsal and lateral.

11. Pigmented spots L-shaped (fig. 18); in haline pools amongst vegetation; near coast ..... *ventralis* Schummel
— Pigmented spots triangular; in woodland soil ..... *modesta* Meigen

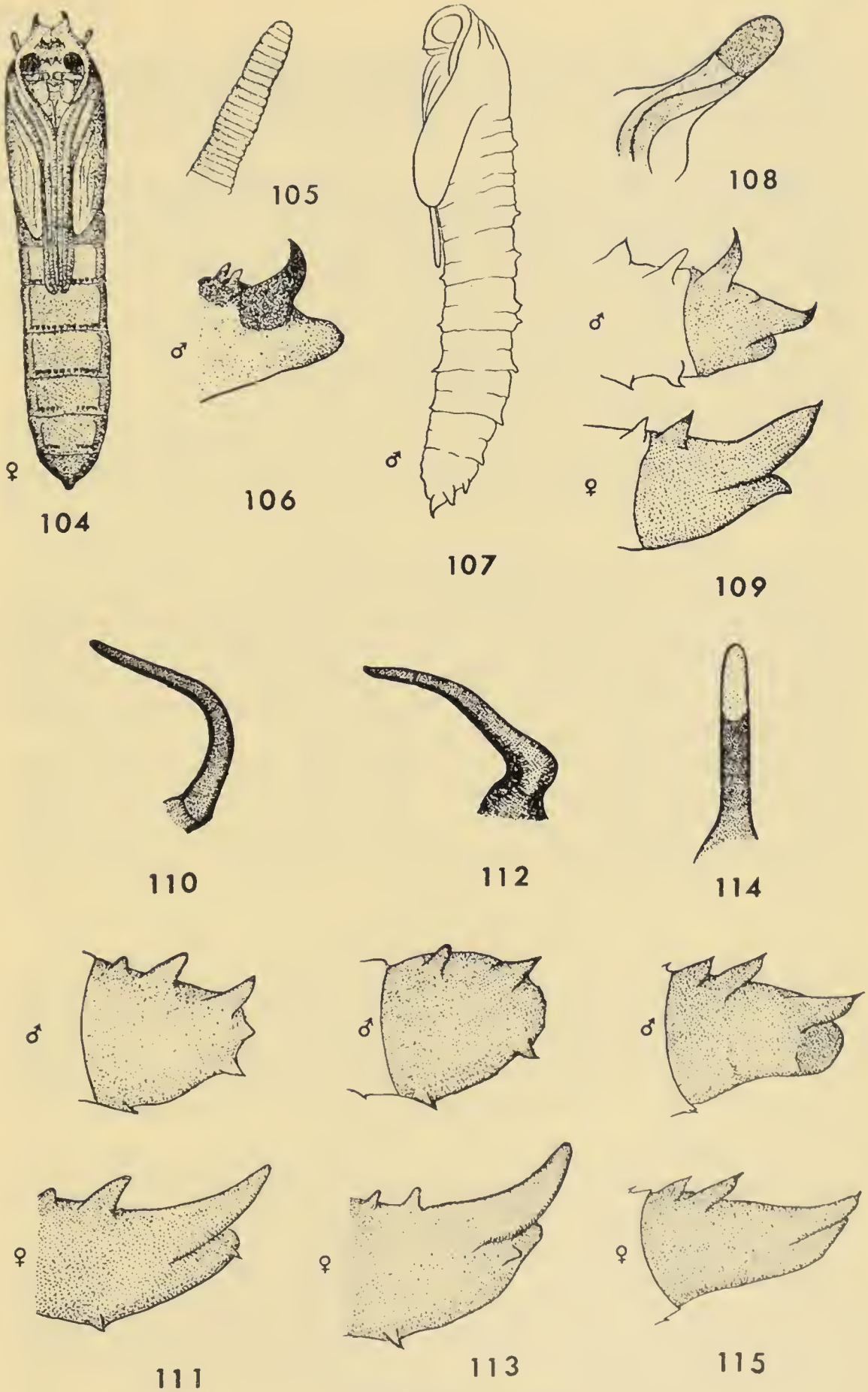
The pupae (fig. 78) remain in the larval tube, and are whitish on the abdomen, yellowish anteriorly and on the anal segment; the wing sheaths, leg sheaths and other appendages becoming blackish when emergence is near. The pronotal horns vary in size and shape, sometimes varying in size between male and female pupae of the same species, as in *L. ventralis*. The pronotal horns of the female pupae of this species are similar to those of the male (fig. 80) but are larger. Length: 12-16 mm (*Metalimnobia*); 9-10 mm (others).

The pupae known to the author can be partially separated into species by the shape of the pronotal horn and by the arrangement of spines on the anal segment, as follows: —

1. Pronotal horns broad (fig. 78); larger, 12 mm or more (*Metalimnobia*) ..... *bifasciata* Schrank *quadrinotata* Meigen (also *quadrimaculata* Meigen)
- Pronotal horns broad or narrower, pupae smaller, 10 mm or less 2
2. Pronotal horns and anal segments as fig. 79 ..... *decemmaculata* Loew
— Pronotal horns and anal segment otherwise 3
3. Pronotal horns broad at base, narrowed distally 4
— Pronotal horns broad, not narrowed distally 5
4. Pronotal horns very long (fig. 93); anal segment of male as fig. 91; that of female fig. 92 ..... *unicolor* Haliday
— Pronotal horns shorter (fig. 81); anal segments fig. 81 ..... *didyma* Meigen
5. Pronotal horns quadrangular from a lateral view (fig. 80); anal segments as fig. 80 ..... *ventralis* Schummel
— Pronotal horns not quadrangular 6
6. Pronotal horns broader than long 7
— Pronotal horns as broad as long, or longer than broad ... 8
7. Pronotal horns evenly rounded anteriorly (fig. 82); anal segments fig. 82 ..... *nubeculosa* Meigen
— Pronotal horns angular anteriorly (fig. 83); anal segments fig. 83 ..... *macrostigma* Schummel
8. Pronotal horns as broad as long ..... *flavipes* Fabricius
— Pronotal horns longer than broad (fig. 84); anal segments fig. 84 ..... *tripunctata* Fabricius *modesta* Fabricius

Taphrophila Rondani

Larvae very distinctive (fig. 23); whitish with prominent dorsal and ventral welts; anal segment with two long processes or lobes, the lobes with tufts of short setae; four long anal



Hexatomini (pupae)

FIGS. 104-115.—104, 105, 106, *H. bicolor*, pupa, ventral, pronotal horn, and anal segment; 107, 108, 109, *D. sexmaculata*, pupa lateral, pronotal horn, and anal segments; 110, 111, *A. ochracea*, pronotal horn and anal segments; 112, 113, *E. ocellaris*, pronotal horn and anal segments; 114, 115, *P. nemoralis*, pronotal horn and anal segments.

papillae. In silken tubes on submerged stones in running water; very common in fast flowing limestone streams, but the larvae do also apparently occur in more acid and slowly moving water. Length: 10-12 mm.

Pupae whitish, head, thorax, and thoracic appendages and anal segment yellow; pronotal horns very characteristic, each horn consisting of a darker base from which arise seven whitish tapering processes and one club-shaped process; one of the tapering processes arises from the club-shaped one (fig. 90); anal segment of male with one large pair of spines (fig. 91); that of female with a pair of smaller spines (as fig. 92); in the larval tube. Length: 6-7 mm (pronotal horns nearly 1 mm).

One species, common along rivers and streams ..... *vitripennis* Meigen

Hinton (1957) gives a detailed account of the structure and function of the pronotal horns.

Thaumastoptera Mik

Larvae (fig. 27) whitish or greenish-white; yellowish and pubescent on the thoracic segments; anal segment emarginate from a dorsal view, the margins with short but dark and conspicuous hairs (fig. 28); in a dark grey or blackish hardened elliptical flattened case (fig. 27) amongst detritus in limey mud near small woodland streams. Length: 6-7 mm.

Pupae yellowish, pronotal horns long and curved towards apices, slightly dilated apically; legs sheaths long (fig. 85); in the larval case. Length: 5 mm.

One species, local but not uncommon in woodlands ... *calceata* Mik

Lenz (1920a) gives an exhaustive account of the larva and pupa.

Elliptera Mik

The retention of *E. omissa* on the British List is due to the record of empty pupal skins found by Dr. F. W. Edwards near Pateley Bridge, Yorkshire. The pupal skins are not apparently preserved in the British Museum (Natural History). The details of the immature stages have been taken from Alexander (1920) after Mik (1886).

The larvae and pupae occur in elongated silken cases, about 10 mm long, the cases being found on wet walls of wooden shutes or runways carrying water, or on wet cliffs or rock.

Larvae (fig. 26) greenish-white, depressed, welts on dorsum of abdominal segments 3-9, the welts having thickly set blackish "points", ventral welts without these points. Spiracular disc and anal segment with four lobes (fig. 25), the posterior surfaces narrowly lined with black, and with long greyish marginal hairs; spiracles elongated. Length: 7 mm.

Pupae (fig. 86) greenish white, anterior parts darker; pronotal horns large characteristic, bright yellowish-white, dorsal side smooth, ventral side with two furrows converging towards apices,

margins finely dentated or notched (fig. 87); segments 3-7 with dorsal and ventral welts. Length: 6·5 mm.

One species ..... *omissa* Egger

The pronotal horns of the pupa have been described as ear-shaped; it should be noted that the pronotal horns of *Lipsothrix* (p. 205) also resemble a pair of ears in the pupal skin. Further discussion on this similarity is given under *Lipsothrix*.

Helius St. Fargeau and Serville

Larvae (fig. 24) covered with dense dark brown or yellowish-brown pubescence, sometimes iridescent; ventral welts present; four anal papillae, the tips of which are elongated; four subequal anal lobes, and with a fifth reduced dorsal lobe, all lobes with narrow blackish lines on posterior surfaces (fig. 22); in marshy soils or semi-aquatic. Length: 15 mm.

Pupae brown, pronotal horns elongated, rather dilated towards apices (fig. 89); anal segment of male with six dorsal spines, and two large anal spines; the anterior and postero-dorsal spines being directed laterad, the medio-dorsal spines being directed dorsad (fig. 88); female anal segment similar but with cerci and sternal valve sheaths; anal spines shorter (fig. 88). Length: 10 mm.

Three species, of which *longirostris* Meigen is the most common and most widely distributed; larvae of *flavus* Walker and *pallirostris* Edwards have occurred between the leaves of marsh plants, such as *Iris* and *Typhae*. The larvae of all three species are very similar. Only the pupa of *longirostris* has been examined.

Pediciini

For a summary of the generic characters of the adults and larvae see Brindle (1963). With the exception of *Ula,* the known larvae form three well defined groups of active carnivores, the groups correlated with the three genera. *Ula* is distinctive and very different from the other genera in most features.

Pedicia Latreille

The larvae of the subgenera, *Pedicia* s.s., *Crunobia* Kolenati, and *Amalopsis* Haliday, do not appear to be sufficiently distinctive to be described separately. The larva most often found is that of *Pedicia rivosa* (Linnaeus) (fig. 29) which is unmistakeable; it is very large, whitish, darkened dorsally on the anterior segments, and very retractile; the head is constantly being exserted and retracted during movement. The larvae of *occulta* Meigen and *straminea* Meigen are light brown, due to the colour of the rather sparse pubescence, and that of *littoralis* is probably similar. In *rivosa* the lateral parts of each welt is developed as a conical tubercle, but the welts of *occulta* and *straminea* are not so well developed. Four elongated anal papillae. Spiracular disc small (as fig. 32). All in semi-aquatic or aquatic habitats, such as

marshy soils, semi-aquatic mosses, or freely aquatic under stones in the bed of small streams. Length: 45 mm (*rivosa*); 25 mm (*occulta*); 15-18 mm (*straminea*). (Probably *littoralis* is rather larger than *occulta*.)

Only the pupa of *rivosa* has been examined (figs. 94-95); enclosed in a substantial silken tube covered with detritus; the pronotal horns are depressed, with sinuate apertures dorsally, the exact shape of which varies (figs. 96, 97). Length: 26-28 mm (pupae of *occulta, straminea,* and *littoralis* probably measure between 15-20 mm).

Four species as given above, all widely distributed.

Trichyphona Zetterstedt

Larvae (fig. 30) whitish or yellowish, distinctive by the form of the anal segment (fig. 34); four elongated anal papillae. The cuticle is covered with short pubescence, much more dense than in *Pedicia*. In marshy soils (*immaculata*) or in sphagnum bogs or acid marshes (*immaculata, unicolor, schummeli*). Length: 15 mm (*immaculata, unicolor*); 11 mm (*schummeli*).

Pupae with abdomen greyish or greyish-white; the welts are not well developed, being without numerous spicules, but they are darker than the rest of the cuticle; anterior parts of pupae and anal segment yellowish or brown; in silken tubes covered with detritus. Pronotal horns short and broad, without a distinct stem (figs. 101). Anal segment of male with one pair of spines, that of female without spines (fig. 100). Length: 8-10 mm (*immaculata, unicolor*). That of *schummeli* has not been obtained but probably measures about 6-7 mm.

Three species as given above, of which *immaculata* is by far the most common and widely distributed species; the other two species are local.

Dicranota Zetterstedt

The subgenera, *Dicranota* s.s. and *Paradicranota* Alexander, do not appear to be distinctive in the immature stages: the larva of the subgenus *Rhaphidolabis* Osten-Sacken, has not been examined. The larvae form a closely similar group of very active carnivores.

Larvae (fig. 31) light brownish-grey to dark grey, the cuticle being covered with dense pubescence, showing marked transverse striations; very retractile, and distinctive in the possession of pseudopods (fig. 33); spiracular disc small (fig. 32) as in *Pedicia*. The larvae of *bimaculata* Schummel, *robusta* Lundstroem, *claripennis* Verrall, and *subtilis* Loew have been examined. Length: 12-15 mm.

Pupae dark or lighter grey, abdomen usually lighter; usually in silken tubes covered with finer material than in *Trichyphona* but the choice of material tends to vary. *Dicranota* larvae living in mosses in lotic water do not apparently construct the pupal tubes unless they have some means of reaching the bank of the

river or stream, so that occasional pupae may be found free. Accordingly this genus is keyed out twice in the pupal key, but further study on this aspect of tube-making should be undertaken. Pronotal horns flattened antero-posteriorly, and with a distinct stem (fig. 103); anal segments as fig. 102. The pupae of *bimaculata* and *robusta* have been examined. Length: 9-11 mm.

Ten British species: in addition to the species included above these consist of: *lucidipennis* Verrall, *pavida* Haliday, *guerini* Zetterstedt, *brevitarsis* Bergroth, *exclusa* Walker, and also *gracilipes* Wahlgren, recorded as British by Coulson (1959).

Miall (1893) gives an account of the life history and structure of the larva and pupae of *bimaculata*.

Ula Haliday

Larvae (fig. 35) yellowish or brownish, segmental constrictions lighter in colour; cuticle with short pubescence showing transverse striations dorsally; anal segment with five almost equal anal lobes, pigmented as fig. 36; four small anal papillae. In various fungi, including *Polyporus squamosus* and *P. betulina*. Length: 10 mm.

Pupae yellowish or brown, with long diverging pronotal horns and long leg sheaths (figs. 98, 99). Length: 6-7 mm.

One species, very common in woodlands ..... *sylvatica* Meigen

Hexatomini

A heterogeneous group, mainly carnivorous and active. The herbivorous larvae are represented by *Dactylolabis,* and both *Pseudolimnophila* and *Oxydiscus* appear to be detritus feeders. In these genera the larvae are much more sluggish and the penultimate segment cannot be inflated. The same characteristics apply to the wood-feeding *Epiphragma* and *Austrolimnophila*. In the other genera the inflation of the penultimate segment is characteristic, though it is not well developed in *Limnophila* s.s., and *Pilaria* larvae (both *nemoralis* and *filata* groups) do not appear to have this characteristic. This inflation is well developed in *Phylidorea, Elaeophila, Hexatoma, Pilaria* (*discicollis* group), and almost always occurs when the larvae are preserved.

For some details of the mouthparts, Brindle and Bryce (1960) should be consulted. Crisp and Lloyd (1954) give an excellent summary of the larval mouthparts and feeding habits.

Hexatoma Latreille

Larvae greenish or brownish-green (fig. 38), with an iridescent pubescence; anal segment with four anal lobes, the fifth being almost absent; ventral lobes rather longer than lateral lobes, and with long hairs or setae at the tip only; long marginal hairs along lateral lobes and along margin of reduced dorsal lobe; each anal lobe has a narrow brown line on the posterior surface, the lines being expanded on the disc (fig. 37). In sand by rivers and

streams in early spring. Brindle (1961) gives an account of the probable life history. The larvae of the two British species can be separated as follows: —

1. Green; pigmented patches on disc below spiracles separated widely, the greatest width being equal to the diameter of the spiracles (fig. 37); larger, 22-24 mm ..... *bicolor* Curtis
— Brownish-green; pigmented patches on disc below spiracles closely approximated, separated by a distance not greater than width of spiracular border; smaller, 18 mm ..... *fuscipennis* Curtis

Both appear to be locally common.

Pupae (fig. 104) greyish or brown; head with two pairs of prominent cephalic spines, directed anteriorly; a smaller pair lower down; an additional third pair is present below eyes; pronotal horns elongate (fig. 105). No distinctions, apart from size have been found between the pupae of the species. Length: 15 mm (*bicolor*); 12 mm (*fuscipennis*).

Dactylolabis Osten-Sacken

Larvae dark yellow or grey, with numerous short dark setae, appearing rather tuberculate; usually darker in appearance due to detritus on the cuticle; four elongated anal papillae; anal lobes four, all subequal in size; usually in hygropetricous habitats, feeding on algae or mosses growing on wet vertical rock faces. The two British species can be separated as follows: —

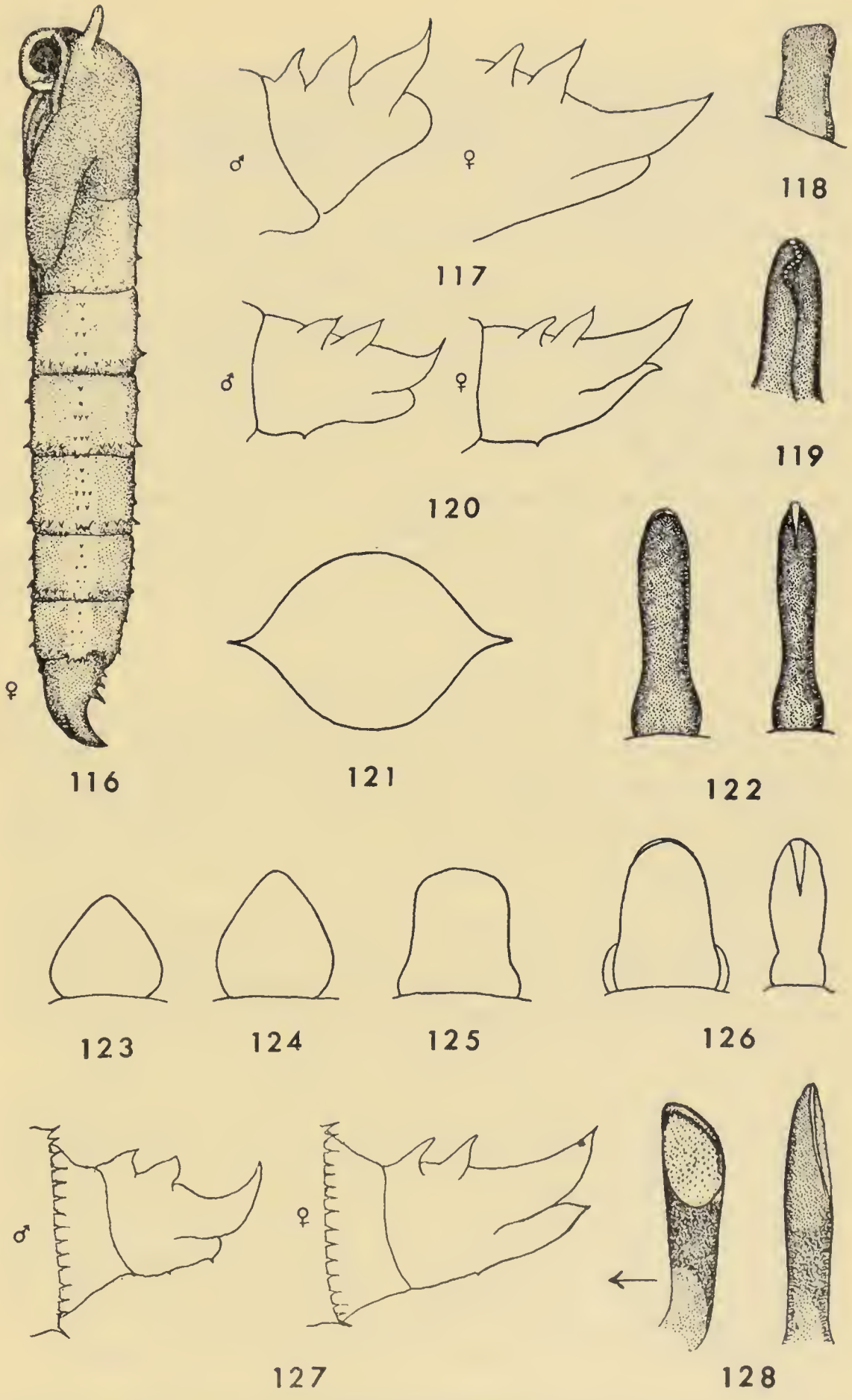
1. Yellowish, each segment with an oblique dorso-lateral black or brown line; posterior surfaces of anal lobes uniformly pigmented or almost so (fig. 43); on gritstone rocks ..... *transversa* Meigen
— Grey; segments with similar oblique black or brown lines; posterior surfaces of anal lobes lighter in colour; darkened around margins (fig. 42); on limestone rocks ..... *sexmaculata* Macquart

Both larvae are usually common where found; the adults of *sexmaculata* have occurred on Raven Scar, below Ingleborough, Yorkshire, which is limestone but which is very dry; in this area the larvae are probably living in the grykes or deep crevices in the limestone rocks, where some degree of dampness exists. Length: 12-14 mm., but rather variable.

Pupae brownish or grey (fig. 107) attached to last larval skin which is fastened to the substratum; cuticle with tubercles; pronotal horns elongated, broadened basally (fig. 108); anal segments as fig. 109. Length: 8-10 mm.

Epiphragma Osten-Sacken

Larvae (fig. 39) yellowish-white or white, with prominent welts on segments 2-7 of abdomen; spiracular disc mainly white, anal lobes white on posterior surfaces, all five rather small but fairly prominent (fig. 40); four rounded or slightly elongated anal



Hexatomini (pupae)

FIGS. 116-128.—116, 117, 118, 119, *L. punctata*, pupa lateral, anal segments, and pronotal horn ventral and lateral; 120, *P. lineola*, anal segments; 121, diagrammatic transverse section of body of pupa of *Phylidorea* showing lateral ridges; 122-126, pronotal horns of *P. abdominalis, P. squalens, P. ferruginea, P. lineola, P. glabricula*; 127, 128, *E. submarmorata*, anal segments, and pronotal horns lateral and ventral (arrow shows ventral direction).

papillae; in dry wood of fallen trees, mainly in the cortical wood just below the surface. Length: 20 mm.

Pupae white on the abdomen, yellowish otherwise; pronotal horns long and curved, with dilated base (fig. 112); anal segments fig. 113. Length: 12 mm.

One species, common in woodlands ..... *ocellaris* Linnaeus

Austrolimnophila Alexander

Similar to *Epiphragma* but smaller, and easily distinguished by the absence of the anal lobes, and by the strongly pigmented spots on the spiracular disc (fig. 41); four rounded anal papillae; in dry wood of fallen trees or branches, mainly just below the surface. Length: 14 mm.

Pupae yellow, white on the abdominal segments; pronotal horn long and curved, but not dilated at the base (fig. 110); anal segments fig. 111. Length: 10 mm.

One species, common in woodlands ..... *ochracea* Meigen

Both *Austrolimnophila* and *Epiphragma* also occur in more rotten and softer wood.

Limnophila Macquart

A very mixed genus, mainly carnivorous. All the subgenera have distinctive larvae, except that *Phylidorea* and *Idioptera* appear to be closely similar, and are dealt with under the former subgenus. The subgenus *Pilaria* has three groups of larvae, regarded as species-groups, all of which have been keyed out separately in both larval and pupal keys, and are dealt with separately below.

A feature of the pupae of most of this genus is that the pleurae are produced laterally, forming a longitudinal ridge which may extend along most of the abdominal segments (fig. 121): this ridge bears the pleural spines which are very prominent in many pupae.

s.g. *Phylidorea* Bigot

Larvae active, whitish, or yellow to brown, with rather thick short pubescence, sometimes iridescent; welts absent and inflation of penultimate segment characteristic; four anal lobes, the ventral pair being the longer, and having much longer marginal hair fringes; spiracular disc white with four black lines, one of which extends on to each of the four anal lobes; four anal papillae, more or less rounded. Semi-aquatic, in marshy soils, saturated soils, mosses, etc. Length: 13-18 mm.

A provisional key to the larvae known to the author is as follows: —

1. Pigmented marks on lateral lobes separated from those on ventral lobes (figs. 44, 45, 50, 51, 52) 2
— Pigmented marks on lateral lobes connected with those on ventral lobes (figs. 46, 47) 5

2. Lateral marks double (fig. 51); larger, 18 mm; whitish; local and uncommon ..... *abdominalis* Staeger
— Lateral marks single (figs. 50, 52); smaller, below 16 mm; yellowish-white 3
3. Lateral marks narrow (fig. 52); smaller, 13-14 mm and associated with sphagnum bogs; but also in lowland districts, near rivers and streams ..... *squalens* Zetterstedt
— Lateral marks broad (fig. 50); larger, 14-15 mm 4
4. Dorsum of anal segment patterned with dark pubescence (fig. 44); common on moors and also near streams and rivers in lowland districts ..... *meigeni* Verrall
— Dorsum of anal segment uniformly covered with pubescence, without such a pattern; common and widely distributed ... *lineola* Meigen
5. Pigmented marks on ventral lobes wider (fig. 46); common, widely distributed ..... *fulvonervosa* Schummel
— Pigmented marks on ventral lobes narrow (fig. 47); common, widely distributed ..... *ferruginea* Meigen

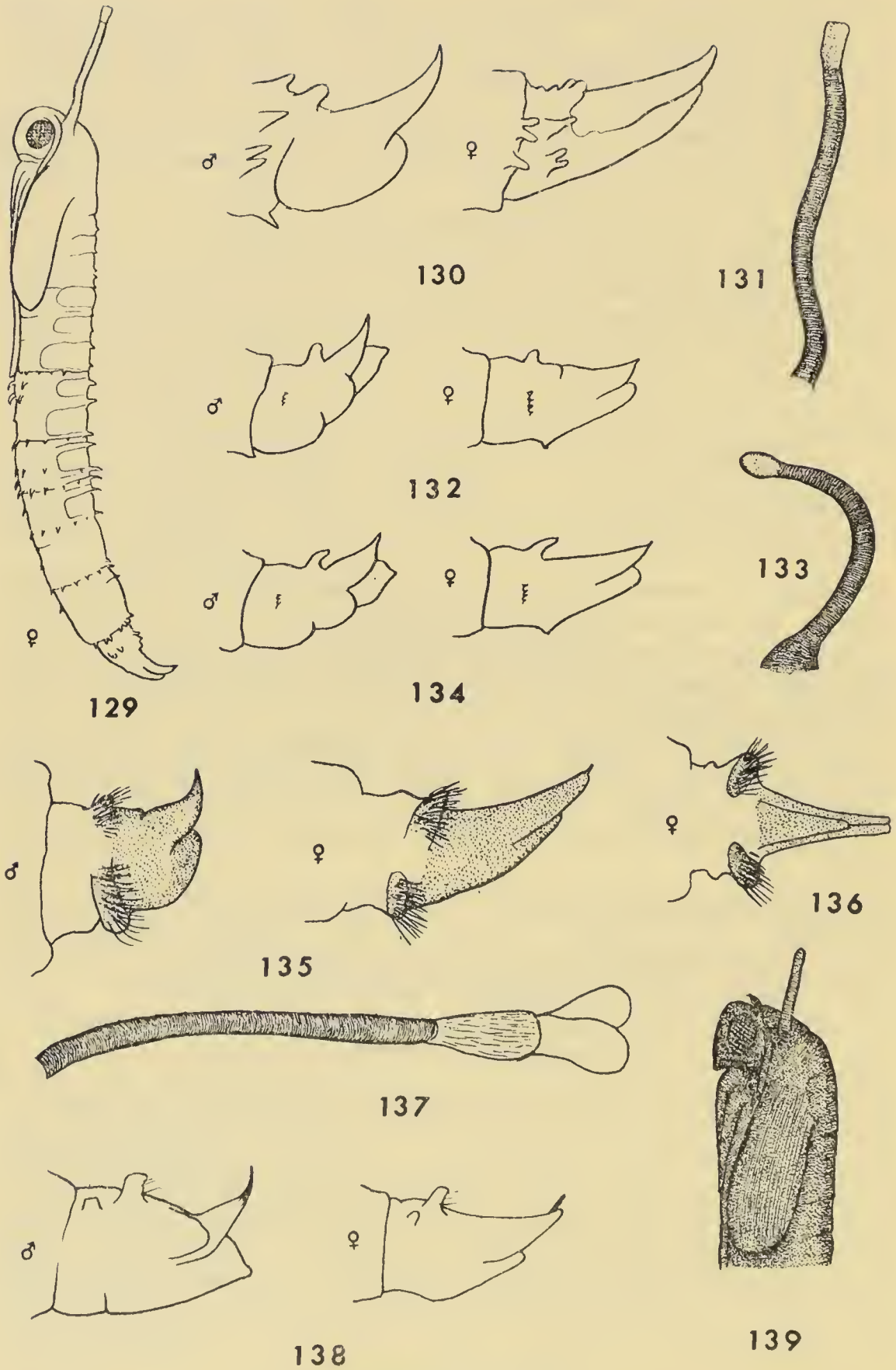
Only one larva of *Idioptera pulchella* has been obtained and this is in poor condition; it appears to be closely similar to *squalens,* but more larvae are required in order to check this (fig. 49). The larvae of *glabricula* also appear to be similar to *squalens* in external features.

Pupae brown, dark brown or blackish, distinctive (except *abdominalis*) in having very short and broad pronotal horns. Length: 10-15 mm.

A provisional key to the pupae known to the author is given below: —

1. Pronotal horns elongated (fig. 122); larger, 15 mm or rather more ..... *abdominalis* Staeger
— Pronotal horns short and broad (figs. 123-126) 2
2. Pronotal horns triangular in shape (figs. 123, 124) 3
— Pronotal horns not triangular in shape (figs. 125, 126) ... 4
3. Pronotal horns equilateral (fig. 123); smaller, 10-12 mm in length ..... *squalens* Zetterstedt
— Pronotal horns longer (fig. 124); larger, 13-14 mm in length ... *ferruginea* Meigen
fulvonervosa Schummel
4. Pronotal horns evenly rounded at tip (fig. 126); smaller, 10-12 mm ..... *glabricula* Meigen
— Pronotal horns broadly rounded at tip (fig. 125); larger, 13-14 mm ..... *meigeni* Verrall
lineola Meigen

The larvae and pupae of the following are apparently unknown, though some species are common in the adult stage: — *heterogyna* Bergroth (rare); *phaeostigma* Schummel (Scotland); *dispar* Meigen (Southern England); *aperta* Verrall (widely distributed).



Hexatomini (pupae)

FIGS. 129-139.—129, 130, 131, *P. discicollis*, pupa lateral, anal segments, and pronotal horn; 132, 133, *P. filata*, anal segments and pronotal horn; 134, *P. batava*, anal segments; 135, 136, 137, *P. lucorum*, anal segments, anal segment ventral, and pronotal horn; 138, 139, *O. minuta* (non-British) anal segments and anterior of pupa (after Alexander, 1920).

s.g. *Elaeophila* Rondani

A very distinctive larval type; active, carnivorous; four long cylindrical anal lobes, tapering distally (figs. 53, 54); spiracular disc small, spiracles small; four small rounded or slightly elongated anal papillae. The cuticle, including that of the lobes, is covered with rather sparse dark pubescence, but the density of the pubescence varies in the different larvae. *E. maculata* and *submarmorata* have sparse pubescence and they are white, with the gut showing clearly; *E. verralli* is smaller and darker, and the gut is not plainly visible. Brindle and Bryce (1960) give a key to some of the larvae based on mouthparts. All semi-aquatic, in sand or soil by edges of streams and rivers. Although the length of the larvae does vary, the species can be approximately separated by the size, since *maculata* is always the largest and *verralli* the smallest. Length: 12 mm (*verralli*); 13 mm (*trimaculata*); 14 mm (*apicata, submarmorata*); 15 mm (*maculata*).

Pupae blackish, with conspicuous spines on the segments, (fig. 127); pronotal horns long, rather flattened laterally, and characteristic in shape (fig. 128). Length: 8 mm (*verralli*); 9 mm (*trimaculata, apicata, submarmorata*); 10-11 mm (*maculata*).

Five species, as given above, all common along streams and rivers; *trimaculata* also occurs in sphagnum bogs. *E. mundata* Loew is thought to be a variety of *submarmorata* (Coe, 1950).

s.g. *Limnophila* s.s.

Larvae yellowish or brown, lighter ventrally and between the segments; cuticle with dense pubescence, rather iridescent; anal segment with four subequal lobes, which are yellowish posteriorly, but darkened apically (figs. 55, 56); four elongated anal papillae (fig. 57); in marshy soils or semi-aquatic, often common in sand or soil by the edges of streams and rivers in early Spring. Length: 20 mm.

Pupae (fig. 116) brown or dark brown, with prominent abdominal spines, those on the pleurae being tuberculate; pronotal horns rather short and broad, apical aperture sinuate (figs. 118, 119); anal segment with long spines (fig. 117). Length: 17 mm.

Two species, of which *punctata* Schrank is by far the most common and widely distributed; *pictipennis* Meigen is uncommon and has not been reared in the present study.

s.g. *Pseudolimnophila* Alexander

Larvae whitish or yellow, anal segment darker, the exact colour apparently depending on the type of soil, and part of the colour at least may be caused by colouring matter from the soil affecting the pubescence on the body; lateral anal lobes short, ventral lobes long and almost parallel-sided; all lobes blackish on posterior surfaces, and with very long marginal yellow hairs (figs.

60, 61). A feature are the long parallel-sided anal papillae, which are sometimes distorted, and which are white or yellow. In saturated soils or in marshy soils. Length: 14-16 mm.

Pupae dark brown or black, lighter along pleurae; anal segment with prominent transverse ridges bearing numerous long dark hairs (figs. 135, 136). The pronotal horns are characteristic (fig. 137) but the two apical flaps may be broken off in pupal skins. In this case the anal segments may be used to separate the pupal skins of this species from those of *discicollis,* the only other common pupae likely to be confused with *lucorum,* on account of the size and the long pronotal horns. Length: 11-12 mm (pronotal horns 3·5-4 mm).

Two species, of which *lucorum* Meigen is the most common and widely distributed species: *sepium* Verrall has not been reared in the present study.

Hinton (1954) gives an account of the structure and some functions of the pronotal horns.

s.g. *Pilaria* Sintenis

Three distinct larval and pupal types, as separated in the key, and regarded here as species-groups.

discicollis group

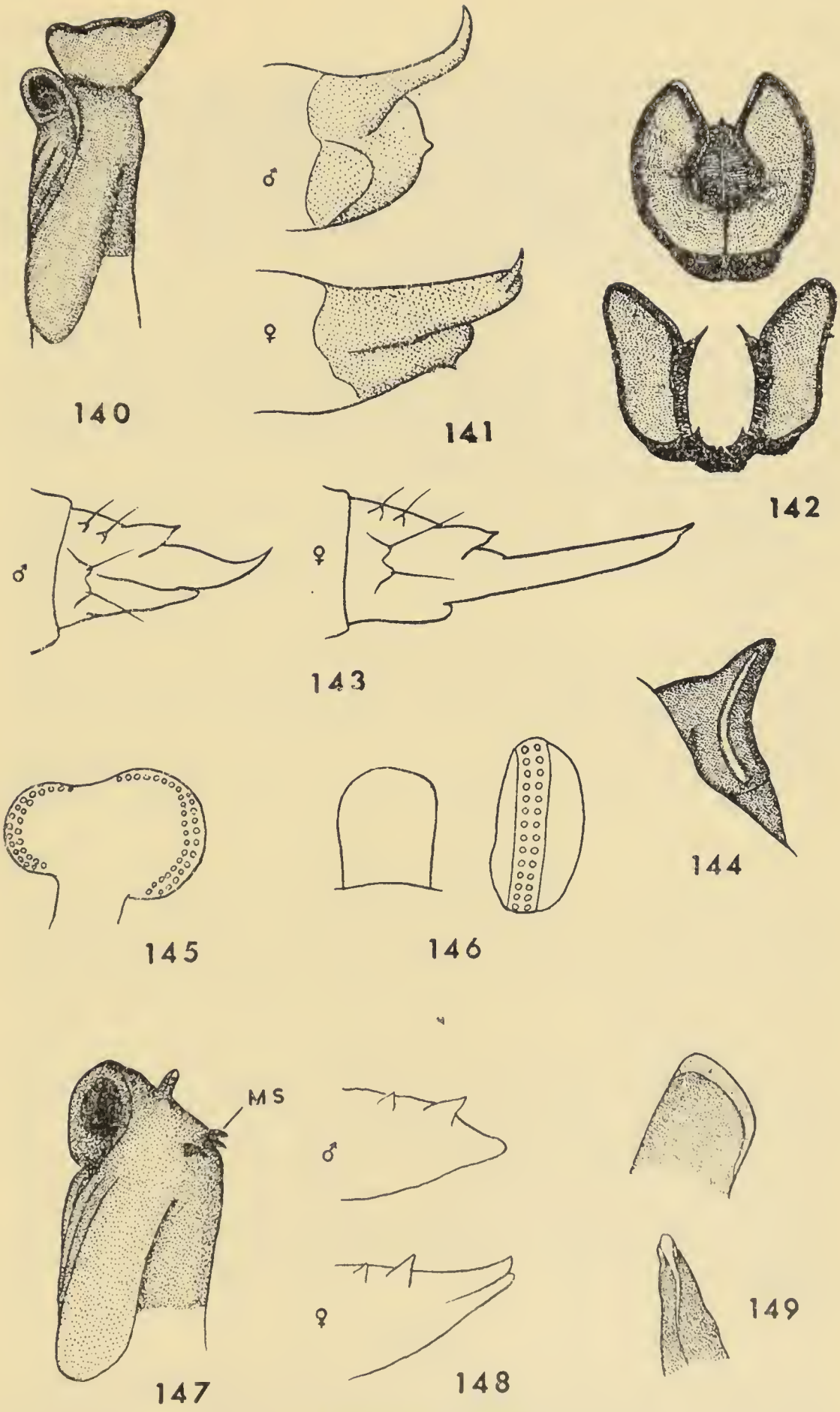
Larvae whitish or yellow, sometimes darkened posteriorly; cuticle with fairly dense pubescence which may show transverse striations; anal segment distinctive (fig. 59); lateral lobes short, ventral lobes long, darkened on posterior surfaces; marginal hairs much longer on ventral lobes; four elongated anal papillae (fig. 58); in marshy soils, or in saturated soils, sometimes along with *lucorum.* Length: 20 mm.

Pupae brown to blackish (fig. 129); abdominal segments with numerous spines; anal segment with tuberculate spines, some being double; male anal spines very long; sternal valve sheath of female almost as long as sheath of cerci (fig. 130); pronotal horns long, apical part rather rectangular (fig. 131). Length: 15 mm (pronotal horns 2·5-3 mm).

Four species, of which *discicollis* is very common and widely distributed; *scutellata* Staeger (uncommon) has been reared once, and the larvae appears to be similar to *discicollis.* The larva and pupa of *meridiana* Staeger (uncommon) and of *fuscipennis* Meigen (rare) are not known. The larva of *meridiana* should be much smaller than that of *discicollis.*

nemoralis group

Larvae yellowish or whitish-yellow; pubescence short; anal segment with four subequal anal lobes and a reduced fifth dorsal lobe, marginal hairs short (fig. 63); four small rounded anal papillae; in a wide range of habitats, ranging from damp woodland soils to saturated soils, or in sand or soil by edges of rivers and streams. Length: 10-12 mm.



Eriopterini (pupae)

FIGS. 140-149.—140, 141, *L. errans*, pupa lateral and anal segments; 142, *L. errans*, pronotal horns as seen from above, top figure shows horns of pupa, lower figure shows horns of pupal skin; 143, 144, *Gn. lugubris*, anal segments and pronotal horn; 145, 146, pronotal horns of *G. lateralis* and *G. alboscutellata* (after Bangerter, 1928, 1930); 147, 148, 149, *G. lucidula*, anterior part of pupa, anal segments, and pronotal horns. (M.S.= mesonotal spines.)

Pupae brown to blackish, abdominal segments with spines but the spines not particularly numerous; anal segment with three pair of spines (fig. 115); pronotal horns elongated, slightly broader at base, apical third lighter in colour (fig. 114). Length: 9 mm.

Two species, of which *nemoralis* Meigen is common and widely distributed. Although the adult of *adjuncta* Walker is not rare, this species has not yet been reared.

filata group

Larvae white, the anal segment being distinctive since the anal lobes appear to be permanently closed, so that the anal segment is conical, with an apical tuft of hairs (fig. 62); in marshy soils, or in sand or soils by edges of streams and rivers. The two British species may be separated as follows: —

1. Smaller, 8-10 mm, concave inner margin of mandible serrated ..... *filata* Walker
— Larger, 14-15 mm, concave inner margin of mandible smooth ..... *batava* Edwards

Pupae brown or blackish, spinous; anal segment with dorsal spines tuberculate; anal spines of male large; a row of small spines laterally (figs. 132, 134); pronotal horns long, often curved, spatulate apex lighter in colour (fig. 133). The pupae may be separated as follows: —

1. Smaller, 7 mm in length ..... *filata* Walker
— Larger, 9-10 mm in length ..... *batava* Edwards

Oxydiscus de Meijere

Larvae yellow or whitish-yellow, rather slender; anal segment with four obvious anal lobes; marginal hairs very long, especially those on ventral lobes; posterior surfaces of lobes and disc pigmented with characteristic markings (fig. 64); in marshy soils. Length: 8-10 mm.

Pupae probably brownish or blackish, and spinous. No pupa of this genus has been examined, and the supposed pupa of the American species, *Oxydiscus* (=*Adelphomyia*) *minuta* Alexander, is figured in the present paper (fig. 138, 139), after Alexander (1920). If the British pupae agree, the distinctive character seems to be the truncated dorsal spines. Length: probably 6-7 mm.

Five British species, of which only *senilis* Haliday has been obtained as larvae but no pupae or pupal skins have yet been obtained.

Eriopterini

The larvae of this tribe are not so frequently obtained by general collecting as the larvae of the Hexatomini; this is partly on account of their smaller size, and also because they are much less active, being herbivorous; this tribe is as yet the least well known with regard to the immature stages. Larvae of certain species can, however, be found in large numbers at certain times.

The larvae are often more slender than those of the Hexatomini; the penultimate segments cannot be inflated, and the spiracular disc and anal lobes are typically heavily pigmented. A common feature is that the anal segment is constricted basally, and dilated distally so that this segment is often much more narrow at the base than the previous segment. There are usually five almost equal or equal anal lobes, *Gonomyia* being unusual in having very short and inconspicuous lobes.

The pupae often resemble those of the Limoniini in having the abdomen lighter in colour, though the pupae may be all yellow. The distinctive feature in almost all the pupae is the presence of spines, setae, or tubercles on the mesonotum which is darkened dorsally. The anal segment may have no spines, a few spines, or several; a feature of *Ormosia* is that the antero-dorsal spine is single and not paired, so that the five dorsal spines form a pentagon (as described by Alexander, 1920). Five dorsal spines also occur in *Rhypholophus* but the single spine is in this genus represented by a small black tubercle.

Lipsothrix Loew

Larvae (fig. 65) yellowish or white, elongated and slender, with protuberant welts; four distinct anal lobes, pigmented as fig. 66; dorsal lobe almost absent; four small anal papillae; in decayed wood of trees or branches, either just below the surface or deeper in softer wood. Length: 20-24 mm.

Pupae yellowish, whitish on abdomen, segments smooth except for welts; anal segment with one pair of anal spines, those of male very long (fig. 141); pronotal horns characteristic, the two horns forming a cup-shaped structure in the pupa (figs. 140, 142 upper); after the adult has emerged the two horns separate, and they then resemble a pair of ears (fig. 142, lower). Pronotal horns yellow, with black margins. Length: 14-16 mm.

Five species, of which *errans* Walker and *remota* Walker have been reared; these are the more common species, and are relatively widely distributed. The other species are *ecucullata* Edwards (rare, Scotland), *nigristigma* Edwards (rare, Lancashire), and *nervosa* Edwards (locally common, Hants and Devon).

The yellow pronotal horns resembling ears may be a source of confusion between pupal skins of this genus and those of *Elliptera omissa* (Limoniini). Mik (1886) apparently described the pronotal horns of this pupa as being ear-like, and they are also yellow in colour. However, pupal skins of *Elliptera* should always be found half way out of the silken cocoons, in hygropetricous habitats, and the shape of the horns is different (see fig. 87). The pupal skins of *Lipsothrix* should always be found half way out of wood, normally in dry wood but occasionally in much wetter wood. There is no pupal case.

During the present study a log of wood was found partly immersed in a pool beneath a small waterfall in Borrowdale, Cumberland. Skins of the pupae of *Lipsothrix* were found pro-

truding from the wood, and subsequent investigations produced several pupae and full grown larvae of *L. errans*. The log had evidently fallen in the water from the bank at some time but the larvae apparently were feeding normally in spite of the fact that the wood was consequently sprayed by water. The interesting sequel to the wet conditions was that a number of *Dicranota* larvae had invaded the wood and were feeding on the *Lipsothrix* larvae, a type of food which is unusual for *Dicranota* owing to the difference in habitats normally occupied by the two larvae.

Gnophomyia Osten-Sacken

Larvae yellow to white, slender, anal segment narrowed at base, and expanded distally; anal lobes with a characteristic pigmented pattern (fig. 67); four small anal papillae; under the bark of dead willows and poplars (possibly other trees) where moisture occurs, often in association with larvae of *Pachygaster, Phaonia* and *Lonchaea*. In these trees the inner part of the bark tends to form flakes and the larvae are typically between these flakes. Length: 14-15 mm.

Pupae yellow, abdominal segments white, except for anal segment; anal segments distinctive, lateral and dorsal spines mainly represented by tubercles from each of which arises a long seta; male with one pair of strong dorsal spines and one pair of anal spines; female with one pair of dorsal spines; cerci sheaths very long; sheaths of sternal valves almost absent (fig. 143); pronotal horns triangular (fig. 144). Length: 12 mm.

One species, local but common where found ..... *lugubris* Zetterstedt

Gonomyia Meigen

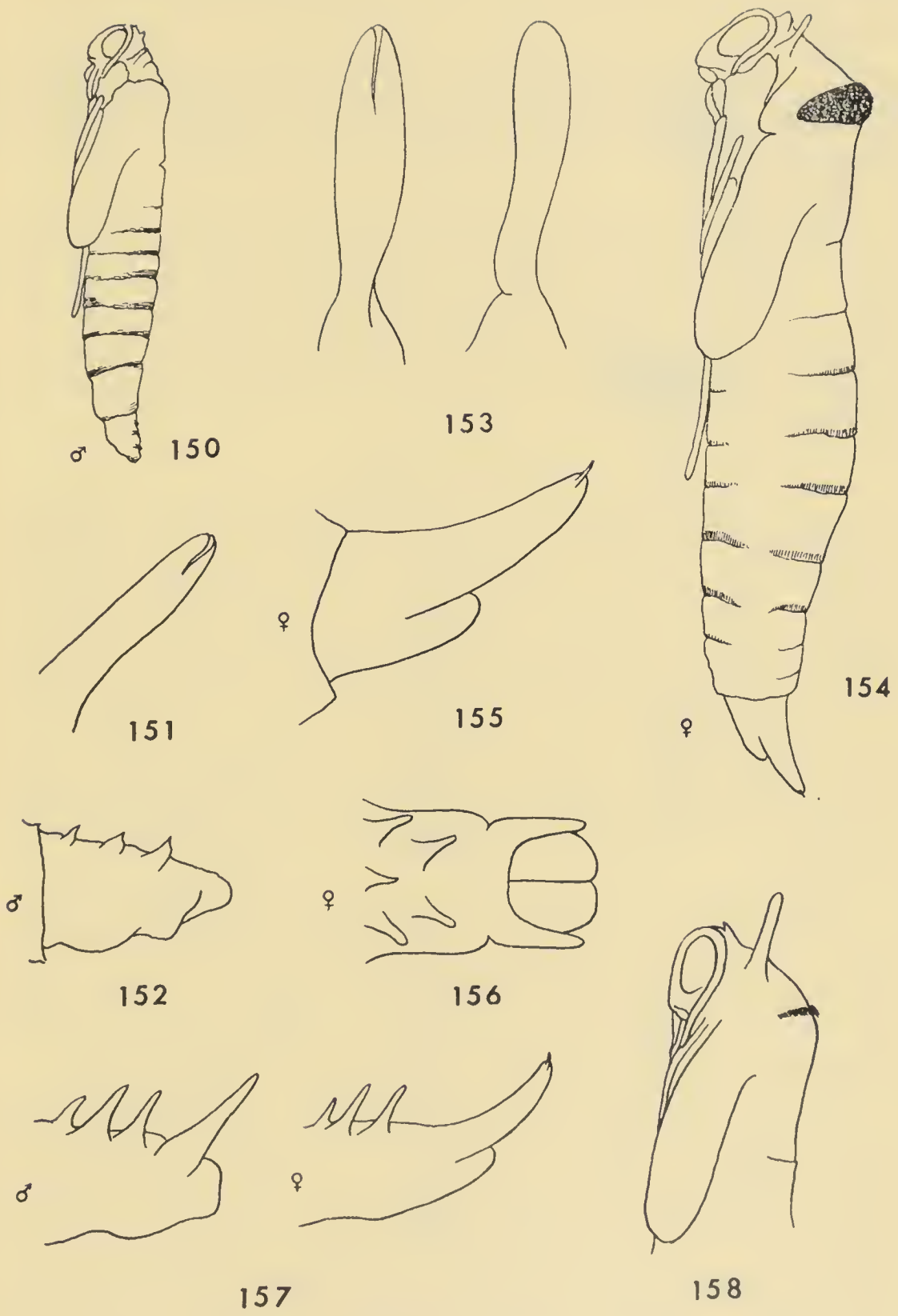
Yellow, slender larvae, anal segment narrowed basally, expanded distally; posterior surface of anal segment without obvious lobes, but very heavily pigmented (figs. 68-70); it is not yet known if the larvae of the subgenera show distinctive features, but the known larvae are closely similar to each other. Length: 10-12 mm.

Pupae yellow, abdomen lighter, not spinous but with welts and with scattered long setae; mesonotum with prominent spines (fig. 147) or tubercles bearing short setae or hairs; anal segments with small dorsal spines (fig. 148); pronotal horns short, rather flattened, somewhat rectangular laterally (figs. 146, 149), or rounded (fig. 145). Length: 8 mm.

Only the larva and pupa of *G. lucidula* de Meijere have been examined; figs. 68, 69, are re-drawn from Bangerter (1928, 1930).

Cheilotrichia Rossi

Only the larva of *C.* (*Platytoma*) *cinerascens* Meigen, and the pupa of *C.* (*Gonempeda*) *flava* Schummel have been examined;



Eriopterini (pupae)

FIGS. 150-158.—150, 151, 152, *C. flava*, pupal skin, lateral, pronotal horn, and anal segment. 153, 154, 155, *S. danica*, pronotal horns lateral and ventral, pupal skin lateral, and anal segment; 156, 157, 158, *O. innocens* (non-British), anal segment dorsal, anal segments, and anterior part of pupa (after Alexander, 1920).

neither larva nor pupa of *C.* (*C.*) *imbuta* Meigen have been obtained.

Larva yellowish, slender; anal segment narrowed basally, dilated distally; four small anal papillae; anal segment with five prominent lobes, the posterior surfaces of which are pigmented as fig. 71. Length: 6-7 mm (the larvae of *imbuta* and *flava* should be smaller).

Pupae brown or yellow (fig. 150); abdominal segments lighter; rather smooth but with welts, and with small spines behind the head; pronotal horns elongate, rather broad (fig. 151); anal segments with three pairs of dorsal spines, no anal spines (fig. 152). Length: 4-4·5 mm (that of *cinerascens* may be rather larger).

Three species, as given above, all widely distributed and common.

Erioptera Meigen

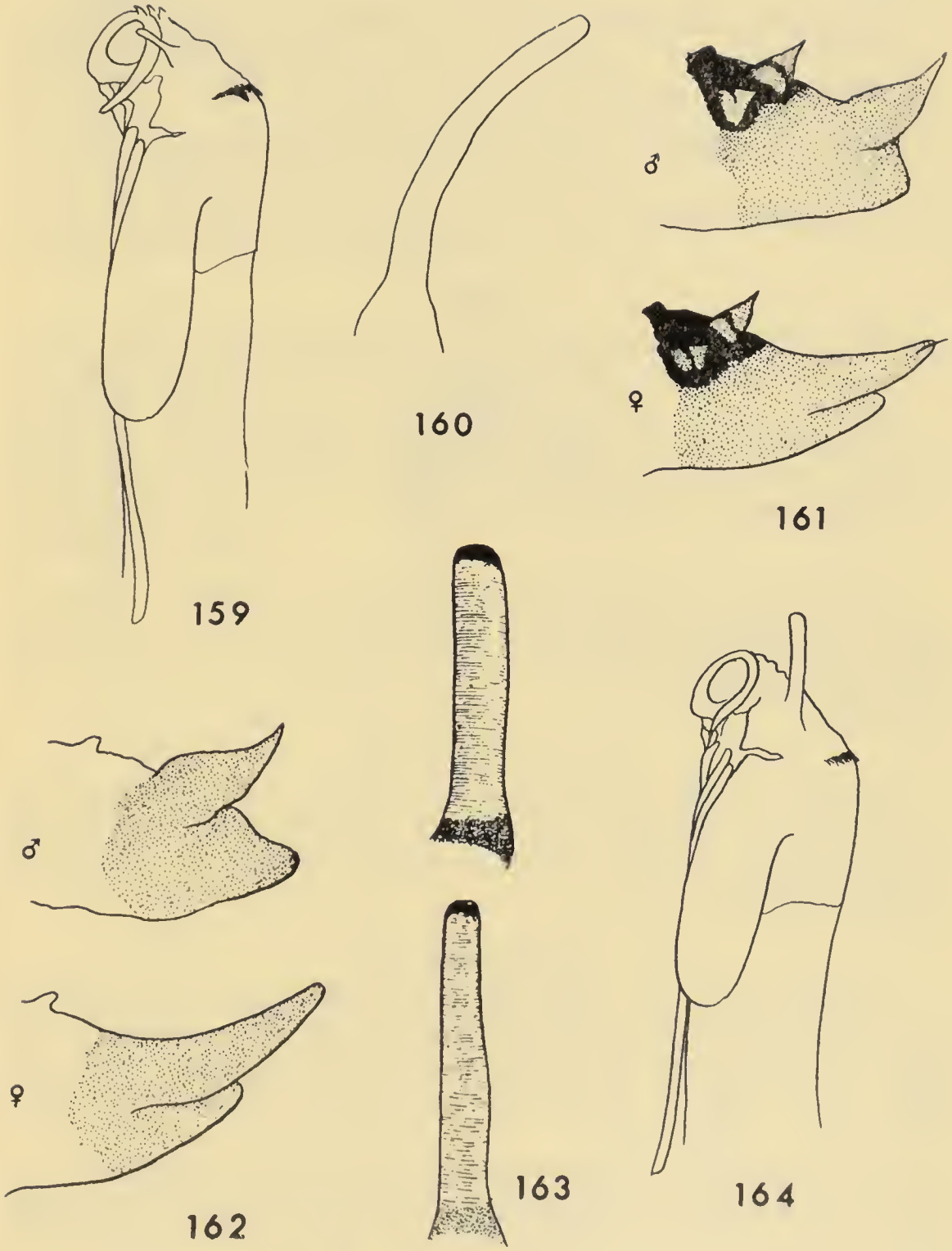
Some of the subgenera of this genus appear to show distinctive features, but others are very similar to each other. Sufficient material has not been examined to deal adequately with this aspect, so that all the larvae and pupae known to the author in *Erioptera,* sensu lato, are included under the present heading. The distinctions and similarities so far known are discussed below.

Larvae yellowish or white, smooth, slender, and with anal segment narrowed basally, and narrower than penultimate segment; anal lobes prominent, posterior surfaces either deeply pigmented and lobes rather shorter (fig. 76) or lightly pigmented and lobes rather longer (fig. 75); four small anal papillae. Length: 10-12 mm.

Pupae yellowish or brown, abdominal segments lighter; smooth except for welts, and with scattered long setae; anal segments with only one pair of spines or none (fig. 162, 167) or with more than one pair (fig. 170); cerci sheaths either strongly curved (figs. 162, 167) or almost straight (fig. 170). Pronotal horns elongated (figs. 163, 166, 168 171). Length: 8-10 mm.

Larvae and pupae of *Erioptera* (*Erioptera*) *flavescens* Linnaeus, *lutea* Meigen, and *fusculenta* Edwards; of *Erioptera* (*Symplecta*) *stictica* Meigen; and of *Erioptera* (*Ilisia*) *maculata* Meigen, and *vicina* Tonnoir have been examined. Of these the subgenera *Erioptera* s.s. and *Symplecta* appear to be closely similar, but those of *Ilisia* are more distinctive. Gerbig (1913) has described the larva of *Erioptera* (*Trimicra*) *pilipes* Fabricius; the anal segment of this larva, from a posterior view, would look like that of *Cheilotrichia* (fig. 71), but with all the lobes completely black, without any median light (unsclerotised) lines or patches; all lobes equally pigmented.

The mesonotal spines and setae are distinct in the pupa of *stictica* (fig. 165), less distinct in *vicina* (fig. 169), and represented entirely by setae in *fusculenta* (fig. 164).



Eriopterini (pupae)

FIGS. 159-164.—159, 160, 161, *Rhypholophus haemorrhoidalis* Zetterstedt, pupal skin, pronotal horn, and anal segments; 162, 163, 164, *Erioptera fusculenta* Edwards, anal segments, pronotal horn (lateral above, ventral below), and pupal skin (anterior part of pupal skin only figured).

Provisional keys to the subgenera would be as follows: —

Larvae

1. Anal lobes completely black on posterior surfaces; all lobes equal in size ..... *Trimicra* Osten-Sacken
— Anal lobes not completely black, all with median unsclerotised area (figs. 75, 76) 2
2. Anal lobes shorter, and more heavily pigmented (fig. 76) ..... *Ilisia* Rondani
— Anal lobes longer, and less heavily pigmented (fig. 75) ..... *Erioptera* s.s., *Symplecta* Meigen

Pupae

1. Anal segments with more than one pair of spines (fig. 170); pronotal horns longer, strongly dilated at base (fig. 171) ..... *Ilisia* Rondani
— Anal segments with only one pair of spines or none (figs. 162, 167); pronotal horns usually shorter and not, or less strongly, dilated at base (figs. 163, 166, 168) ..... *Erioptera* s.s. *Symplecta* Meigen

Neither larva nor pupa of any of the three species of the subgenus *Psiloconopa* Zetterstedt are known.

A total of 25 British species, many of which are common and widely distributed.

Ormosia Rondani

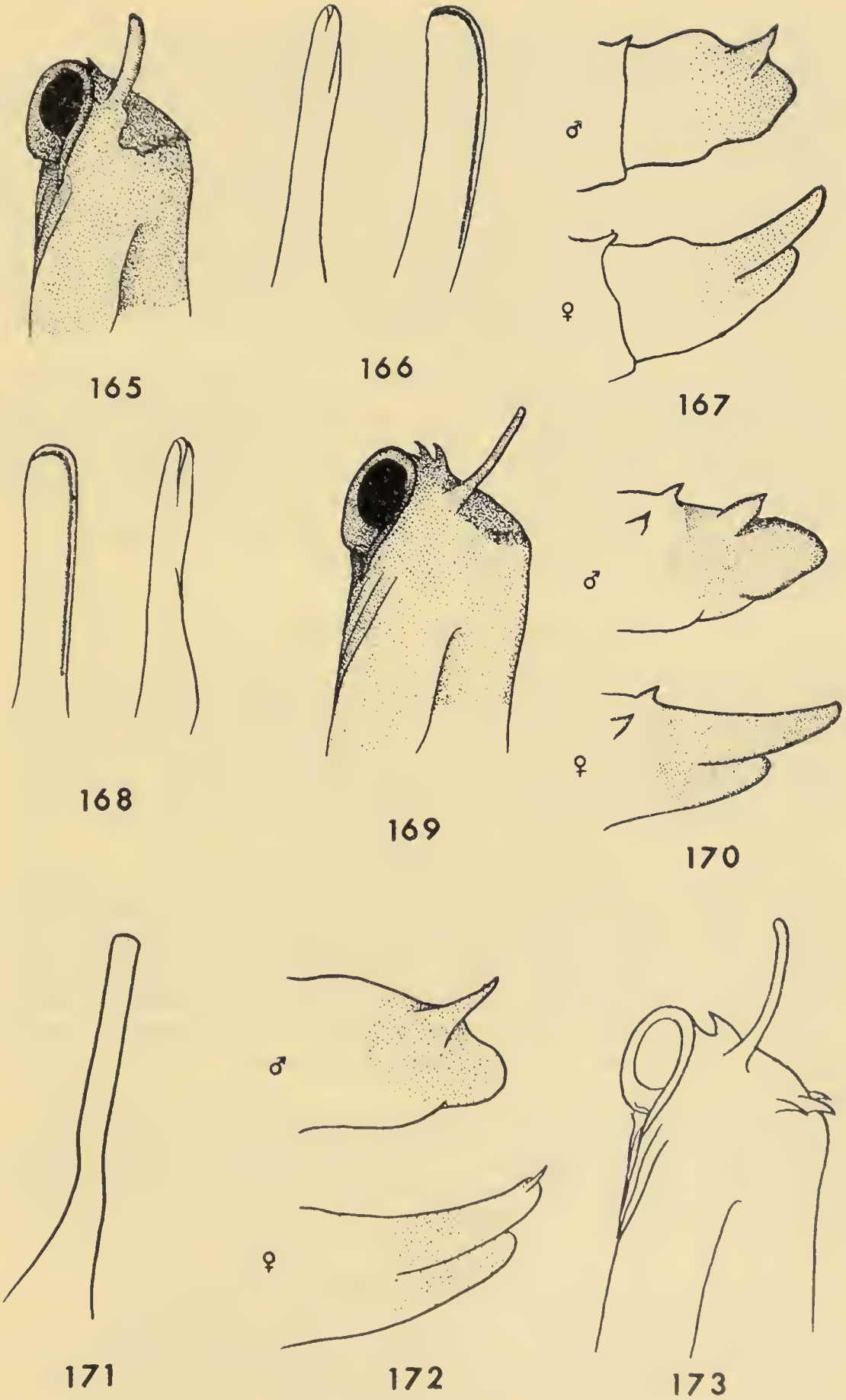
The three subgenera, *Ormosia* s.s., *Scleroprocta* Edwards, and *Rhypholophus* Kolenati, appear to have very distinctive larvae and pupae as separated in the keys, and these are dealt with separately below.

s.g. *Ormosia* s.s.

Larvae yellow or white, slender, anal segment constricted basally, dilated distally; anal segment with five subequal anal lobes, pigmented as fig. 72; four small anal papillae. Only the larva of *O. lineata* Macquart has been examined. Length: 10-12 mm.

Pupae probably yellow or brown with lighter abdominal segments; no pupae of this genus have been seen, but they probably agree with the other Eriopterine pupae. Details below are from Alexander (1920) for American pupae. Mesonotum with setae, more or less well developed (fig. 158); pronotal horns elongated and straight (fig. 158); anal segments with long fleshy spines (fig. 157); or with sclerotised spines; the single antero-dorsal spine is similar to the other spines (fig. 156); anal spines large. Length: probably about 8 mm.

Nine British species, many of which are common and widely distributed.



Eriopterini (pupae)

FIGS. 165-173.—165, 166, 167, *E. stictica*, anterior part of pupa, pronotal horns ventral and lateral, and anal segments; 168, *E. flavescens*, pronotal horns, lateral and ventral; 169, 170, 171, *E. vicina*, anterior part of pupa, anal segments, and pronotal horn; 172, 173, *M. obscurus*, anal segments and anterior part of pupa.

s.g. *Scleroprocta* Edwards

Entirely white, except for the five equal anal lobes which are blackened posteriorly and anteriorly; margins of lobes finely dentated (fig. 77), a rather distinctive larva.

This larva has been reared on three occasions, although only one larva was involved each time; each time *S. danica* Nielsen was reared, a fact which should tend to confirm the identity. This larva is identical with the Eriopterine No. 1 of Alexander (1920, figs. 404, 406); with the *Gonomyia* of Pierre (1924, p. 142, fig. k); and with *Ormosia fascipennis* of Bangerter (1930, fig. 8). Length: 12-14 mm.

Pupae (fig. 154) yellowish, white on abdominal segments; mesonotum with prominent transverse ridge bearing numerous very short setae or spinules; anal segments without dorsal spines but with one pair of anal spines (fig. 155); pronotal horn rather cylindrical, and constricted basally (fig. 153). Length: 8 mm.

Two species, of which only *danica* Nielsen (uncommon) has been reared; *sororcula* Zetterstedt, is rare.

Rhypholophus Kolenati

Larvae very distinctive, with dense yellowish-brown to dark brown pubescence, iridescent; five equal anal lobes with long marginal hairs, and dark brown on posterior surfaces (fig. 73); very common amongst wet leaves in gullies in Spring, or in marshy soils. The larvae appear to undergo diapause from the end of June until later in August when they pupate. Length: 12-14 mm.

Pupae yellowish, white on abdomen, smooth except for welts; anal segment not unlike that of *Ormosia* s.s. in having prominent spines, and a single antero-dorsal spine, but the dorsal spines are broader, and there is a black area around the bases of the spines which includes the single antero-dorsal spine; this latter is represented by a small black tubercle. The other dorsal spines are also partially black (fig. 161); mesonotum with depressed spines (fig. 159); pronotal horns elongated, dilated basally (fig. 160). Length: 8-9 mm.

Three British species, *varia* Meigen, *bifurcata* Goetghebuer, and *haemorrhoidalis* Zetterstedt, of which the first and last species have been reared. All the species are widely distributed and common in Autumn.

Molophilus Curtis

Larvae yellow, very slender, much more slender than in the other Eriopterine genera; anal segment constricted basally so that the segment is narrower than the penultimate one; anal lobes pigmented posteriorly as fig. 74. Although a number of larvae referred to this genus have been obtained, only *M. obscurus* Meigen, and one female near *flavus* Goetghebuer have been reared. Length: 8-10 mm.

Pupae yellowish or brown, abdominal segments lighter in colour, smooth except for welts; characterised by the strong mesonotal spines (fig. 173) and by the long, rather curved pronotal horns (fig. 173); anal segments with one pair of spines (fig. 172). Length: 4-4·5 mm.

Twenty-one British species, many of which are common and widely distributed.

10. Check List of Genera and Species-Groups

CYLINDROTOMINAE

	Larvae	Pupae
Cylindrotoma Macquart	figs. 1, 12	fig. 11
Diogma Edwards	figs. 3, 8	fig. 7
Triogma Schiner	figs. 2, 10	fig. 9
Phalacrocera Schiner	figs. 4, 6	fig. 5

LIMONIINAE

Limoniini		
Limonia Meigen	figs. 13-21	figs. 78-84 92-93
Taphrophila Rondani	fig. 23	figs. 90-91
Thaumastoptera Mik (*Orimarga* Osten-Sacken)	figs. 27, 28	fig. 85
Elliptera Schiner	figs. 25, 26	figs. 86-87
Helius St. Fargeau and Serville	figs. 22, 24	figs. 88-89
Pediciini		
Pedicia Latreille	fig. 29	figs. 94- 97
Trichyphona Zetterstedt	figs. 30, 34	figs. 100-101
Dicranota Zetterstedt	figs. 31-33	figs. 102-103
Ula Haliday	figs. 35-36	figs. 98- 99
Hexatomini		
Hexatoma Latreille	figs. 37-38	figs. 104-106
Dactylolabis Osten-Sacken	figs. 42-43	figs. 107-109
Epiphragma Osten-Sacken	figs. 39-40	figs. 112-113
Austrolimnophila Alexander	fig. 41	figs. 110-111
Limnophila Macquart		
s.g. *Phylidorea* Bigot	figs. 44-52	figs. 120-126
Elaeophila Rondani	figs. 53-54	figs. 127-128
Limnophila s.s.	figs. 55-57	figs. 116-119
Pseudolimnophila Alexander	figs. 60-61	figs. 135-137
Pilaria Sintenis		
discicollis group	figs. 58-59	figs. 129-131
nemoralis group	fig. 63	figs. 114-115
filata group	fig. 62	figs. 132-134
Oxydiscus De Meijere	fig. 64	figs. 138-139

Eriopterini		
(*Neolimnophila* Alexander)		
(*Crypteria* Bergroth)		
Lipsothrix Loew	figs. 65-66	figs. 140-142
Gnophomyia Osten-Sacken	fig. 67	figs. 143-144
Gonomyia Meigen	figs. 68-70	figs. 145-149
(*Rhabdomastix* Skuse)		
Cheilotrichia Rossi	fig. 71	figs. 150-152
Erioptera Meigen	figs. 75-76	figs. 162-171
Ormosia Rondani		
s.g. *Ormosia* s.s.	fig. 72	figs. 156-158
Scleroprocta Edwards	fig. 77	figs. 153-155
Rhypholophus Kolenati	fig. 73	figs. 159-161
Molophilus Curtis	fig. 74	figs. 172-173
(*Tasymolophilus* Skuse)		

Subgenera are only used when the larvae and pupae show distinctive characters.

Brackets indicate genera either unknown or inadequately known in the immature stages, and not included in the present keys or descriptions.

11. Addenda and Corrigenda

An opportunity is taken to draw attention to two errors in the previous paper on the larvae and pupae of the British Tipulinae (Brindle, 1960).

1. *Tipula gimmerthali* Lackschewitz

This species was omitted in the Check List of British Tipulinae (Brindle, l.c., pp. 111-113). The species should have been included along with *livida* and *siebkei* in the additions to the British List since Kloet and Hincks (1945). The species was introduced to the British List by Brown (1947), and is included in Coe (1950). I wish to express my gratitude to Mr E. S. Brown for drawing my attention to this omission.

2. *Tipula brevispina* Pierre and *T. cava* Riedel

It has been noted that the captions to the figures showing the anal segments of these two larvae are interchanged. Fig. 29, given as *brevispina* is really *cava*: fig. 27, given as *cava*, is really *brevispina* (p. 87). In couplet 29 (p. 89) fig. 27 should be substituted for fig. 29 for *brevispina*, and fig. 29 substituted for fig. 27 for *cava*.

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